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Common Spider Mite, *Tetranychus althaeae* v. Hanst. with
particular consideration to the hop as the host 181

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FARBENFABRIKEN BAYER
AKTIENGESELLSCHAFT
Department for Plant Protection
LEVERKUSEN

Investigation of the Biology and Epidemiology of the Common Spider Mite, *Tetranychus althaeae* v. Hanst. with particular consideration to the hop as the host

By Dr. Wilfried Linke, Tetschen (Elbe)

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I. Introduction and Statement of the Problem

From a propagative and economical point of view, the most influential member of the Tetranychidae family is the common spider mite, *Tetranychus althaeae* v. Hanst. The increasing significance of this family has been stressed in numerous publications devoted to it during the past few years. Despite the fact that the common spider mite only occurs periodically, it represents a serious danger to Germany's hop growing districts — a danger which, as a rule, can only be overcome by intensive control measures on the part of the growers.

Although we are acquainted with the main features of this insect's biology and mode of life, there are still several questions yet unanswered. These

questions were the inducement to write this paper, justification of which is supported by the contradictory conceptions in pertinent literature. These varying data on the biology of the insect are comprehensible when considering the dependence of all the vital functions of *Tetranychus althaeae* upon temperature, although the observations made in this connection originate from the most varied climatic zones in conformity with the wide field of propagation. It therefore appeared all the more urgent to establish the connections between temperature and the development of *T. althaeae* under outdoor conditions by separately observing isolated individuals and reproducing the results by means of graphs.

Furthermore, an attempt was made in outdoor experiments to obtain clarity on the effect of the rain as well as the influence of varying supplies of water to the hosts on the development and oviposition of *T. althaeae*. The clarification of several special problems, such as the development of *T. althaeae* at constant temperatures and varying degrees of relative humidity, was tackled in laboratory experiments arranged for this purpose.

With the help of phenomenological-statistical observations made in the stock, the change in the population density of *T. althaeae* and the population-dynamic factors influencing this change were submitted to a critical scrutiny in order to obtain some form of guide for the prediction of the expiration of a gradation.

Even today our knowledge about the relationship between the environments and the life of animal parasites is still far from complete. In view of this, attention in all investigations was concentrated mainly upon establishing the effect of the abiotic factors and their relation to the biological and epidemiological behaviour of *T. althaeae*, insofar as information could be gained which is essential, and thus of direct practical significance, for the assessment and furthering the development of control and prognostic processes.

The investigations on which this paper has been based were carried out partly at the Farbenfabriken Bayer (Leverkusen) Experimental Farm at Höfchen, and partly in the Bavarian hop growing region in the Hallertau.

II. Systematic classification and nomenclature of *Tetranychus althaeae*

The following survey provides information on the systematic classification of the spider mite *Tetranychus althaeae* v. Hanst. discussed in this paper:

Phylum	Articulata	
Subphylum	Arthropoda	
Class	Arachnoidea	
Order	Acari	
Suborder	Trombidiformes	Reuter
Family	Tetranychidae	Donnadieu
Genus	<i>Tetranychus</i>	Dufour
Species	<i>T. althaeae</i>	v. Hanstein

Even today much obscurity still exists about the question concerning the nomenclature and the synonyma of *T. althaeae*. This is to be attributed to the difficulty experienced in recognizing morphological and anatomical details as well as to the different manner of assessing the characteristics essential for systematic classification.

The opinion of Zacher (1949) that *Tetranychus althaeae* v. Hanst., *Tetranychus urticae* Koch and *Tetranychus bimaculatus* Harvey are identical is not shared by all acarologists. McGregor (1951) disputes that *Tetranychus althaeae*

is identical with *T. urticae*, and proves that strictly speaking even *T. althaeae* and *T. bimaculatus* are not of the same species, basing his assertion on differences he has established in the structure of the terminal sensilla of the female palptarsi; he says, however, taking into consideration the shape of the penis as a diagnostic feature, that *T. althaeae* is very similar to *T. bimaculatus*. He opposes the opinion expressed by Massee (1951) that *Tetranychus telarius* L. is synonymous with *T. althaeae*, pointing out that *T. telarius* is quite a different European species which can be easily distinguished from the other. Just the same, the scientific name given in most cases in English literature for the spider mite occurring on hops is *T. telarius*. In addition it should be mentioned that in infection tests I carried out, the linden spider mite, which we refer to as *T. telarius* and which can be easily distinguished morphologically, as well as on the basis of the deviating sizes, from *T. althaeae*, did not continue its development on hops but emigrated within 24 to 36 hours.

Occasionally a new species, *Septanychus* sp., described by McGregor, is referred to in American papers (Batchelor 1950) as a hop spider mite.

In this paper it is intended to use the designation most frequent in German literature, namely *Tetranychus althaeae* v. Hanst.

It is customary in Germany to refer to *T. althaeae* as Rote Spinne, Gemeine Spinnmilbe, Hopfen-, Bohnen-, Eibisch- and Malvenspinnmilbe (red spider, common spider mite, hop spider mite, bean spider mite, marsh mallow spider mite and common mallow spider mite). In foreign literature the designations commonly used are common red spider, hop red spider, two spotted spider mite, roode mijt, *Tetranyque tisserand*, *Araigné rouge* and *Ragno rosso* which, to a certain extent, refer to the genus *Tetranychus* Dufour and other closely related genera (*Eo-*, *Schizo-*, *Paratetranychus* etc.) which are very similar to *Tetranychus* Dufour in their mode of life.

III. Morphology and Anatomy of *Tetranychus althaeae*

Body and Segments

The soft cutaneous oval-shaped body of *T. althaeae* is inarticulated, and can only be sub-divided into two sections by the ringed groove running behind the second pair of legs, namely into the proterosoma with the two front pairs of legs, and the hysterosoma with the two backward pairs of legs (Fig. 1). On the dorsum are six transversal rows of bristles referred to as vertical, scapula, humeral, dorsal, lumbal and sacral hairs. According to the investigations of Thor (1903), the integument consists of superimposed chitin layers excreted by a matrix. The part bearing the two pairs of piercing-sucking mouth extremities is referred to as the gnathosoma. There are far fewer segments in the mouth parts than in the legs. Most of the segments are well fused, and only the tibia and the tarsus are easily perceptible.

The upper jaws are also termed chelicerae, mandibles or jaw feelers. The basal segments of the mandibles are fused to the mandibular plate which is covered dorsally by a skin fold of the gnathosoma. Whereas the *digiti fixi* are reduced to two small points (*digitus fixus* = point of tibia), the *digites mobiles* (*digitus mobilis* = tarsus) are long, supple and stylet-shaped. They are employed to pierce the plant tissues and for this purpose they can be moved forward with the aid of fine muscular fibres.

The lower jaw feelers, also termed maxillary palpi or pedipalpi, consist of five segments, namely trochanter, femur, genu, tibia and tarsus. The last segment but one, the tibia, is equipped with a spur, the tibia spur. The last segment, the conical tarsus, has seven hairs which to a certain extent are modified, namely into a terminal and a lateral cone-shaped sense organ, two needle-shaped cleaning hairs and three ordinary tactile hairs. The hairs are immovable and form part of the sensory organs.

There are eight legs each consisting of six segments and covered by numerous stylets. The tarsi terminate in an empodial apparatus split into six parts. Above this apparatus are two pairs of adhesive hairs with suckers.

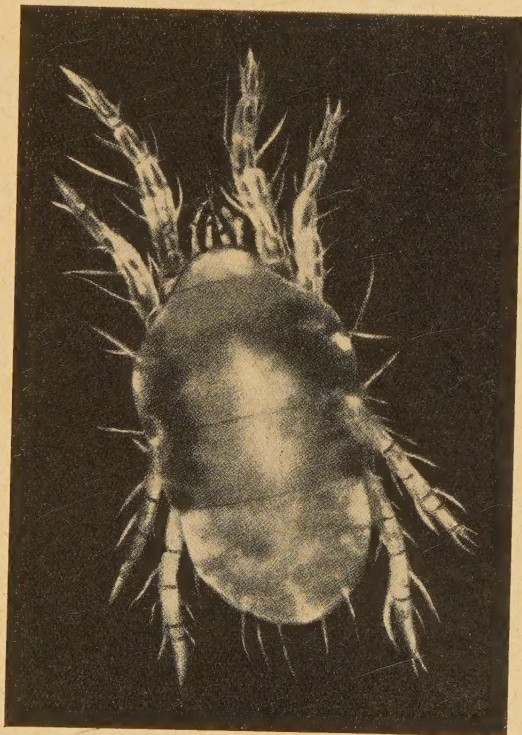


Fig. 1. Female of *T. althaeae*, magnified approx 100 times (Hoed)

On each side of the proterosoma are two stemmata. The retina which is slightly concave at the top is red pigmented, this being the reason why the so-called "eye spots" can be easily seen with the naked eye.

Respiratory organs

Respiration is effected through two simple tracheal trunks entering into two stigmata located close to each other underneath the mandibular plate and inside the body. These are connected to the outside air by tubular apophyses known as peritremata. The structure of the latter is of particular importance in the classification of Tetranychidae.

Spinning glands

The aciniform glands, described by Vitzthum (1943), arranged in pairs and opening in the vicinity of the oral cavity are undoubtedly spinning glands. According to André (1932), the secretion formed during spinning passes into the mouth-opening in small droplets and then flows along the two chelicerae. As a result two silk fibres are formed which later join together. According to measurements taken by Gasser (1951), their diameter is 0.03 to 0.06 μ . The completed web can be seen with the naked eye as a fine, silvery glittering texture of varying expansion on the abaxial surface of the leaf. Whereas this web is only found in most cases between the single leaf ribs when the infestation is only slight, the lower surfaces of the leaves may be completely covered when the degree of infestation assumes large-scale proportions.

Digestive organs

The mouth opening is located underneath the mandibular plate between the pedipalpi. Behind the mouth the alimentary canal leads into a long pharynx followed by the muscular oesophagus which runs into a very wide mid-intestine with four lobular blind sacs on each side.

The stomach blind sacs, when filled, have a dark appearance and can be seen, particularly in the juvenile stage, through the sides of the body.

Excretory organs

To excrete nitrogen, the Tetranychidae have an excretory organ corresponding to the Malpighian tubes. It has the structure of a simple tube and leads into the uroporus. The nitrogen is excreted in the form of guanin (aminooxypurine). This forms ellipsoidal concretions which are bound into a pulpy substance by a liquid product in the excretory tube. The transparent excreta droplets are mostly deposited in the web. Next to them are black concretions of guanin which in this concentrated form does not transmit light.

Circulatory system

The vascular system is open, and there is no heart. The blood is a colourless liquid containing leukocytes. It is stirred up by the movement of the muscles and flows round all the organs.

Genital system

T. althaeae is bisexual and reproduces by ovipositing. Between the genital region, located ventrally in front of the uroporus, and the crescent-shaped genital plate is the genital orifice, which in the case of the female is a cross slit and for the male is a longitudinal slit. The penis, shaped like an unciform, curved tube, is protrusible. The ovarian apparatus is described by Beaumont (1951) for *Metatetranychus ulmi* Koch. He says the ovary is a simple, cyst-like organ. Before being laid, the eggs pass from the ovary into a glandular ovipositing pouch.

Nervous system

The nervous system, combining the brain and the abdomen ganglia, is closely amalgamated into a single ganglia surrounding the oesophagus. The commissures as such are no longer recognizable.

Storage organ

According to investigations carried out by Reiff (1949) on *Paratetranychus pilosus* C. and F., the storage organ assumes a cyst-like structure which partially

incorporates the ovary. It appears to be an organ analogous to the adipose body of the insect.

Embryology

To understand the morphological description of the single development stages of *T. althaeae*, it is necessary to describe briefly the biology of development in general.

T. althaeae, which overwinters as an imago, reproduces oviparously. The six-footed larvae emerging from the eggs and which greatly resemble the fully grown mite, differing chiefly in size, go into the dormant stage after a short time. This is termed the nymphochrysalis. The first eight-legged nymph stage, the protonymph is followed by the deutochrysalis.

The deutonymph which then emerges develops through the final dormant stage, the teliochrysalis, into a puberal imago (prosopon). The complete process of development, with four mobile and four dormant stages, one immediately following the other, is termed epimorphosis.

The egg

Diameter 0.13 mm, spherical. Shortly before hatching, changes in shape may be observed caused by the movement of the larva which bores the egg shell with its mandibles (Gasser 1951) and crawls out of the egg backwards. The hatching process lasts from 6 to 8 minutes.

The sizes of the active stages were determined from several measurements taken by means of an ocular micrometer. The values given below are the averages of ten measurements taken in each case.

Stage	Length-breadth index in mm*	
Young larva	0.15 × 0.11	
Old larva	0.18 × 0.12	
Protonymph	0.24 × 0.14	
Male deutonymph	0.27 × 0.15	
Female deutonymph	0.38 × 0.22	Sexual dimorphism already pronounced
Male	0.29 × 0.16	Strongly reduced abdomen
Young female	0.44 × 0.24	
Old female	0.47 × 0.26	

The *T. althaeae* female weights 0.0108 mg. This value represents the average for 45 females of medium age each weighed twice on a microbalance. In order to prevent the female mites from wandering off while being weighed, they were placed on a sheet of tin foil coated with vaseline.

The dormant stages are characterized by a cessation of sucking, immobility and unusual behaviour. After the active stages have found a protected site, chiefly in the vicinity of leaf ribs, they firmly attach themselves to the substrate by means of their silk fibres (Gasser 1951). According to Vitzthum (1943),

* Length measured as far as the front edge of the collar.

the interior of the body and its segments are then set free from the integument and contracted. As a result the empty integuments take up a position folded downwards assuming the appearance of short stumps. During the dormant stages the new nymph skin is formed. The ecdysis itself is initiated by the formation of a cross slit in the back of the old nymph skin. The nymph then releases itself from the two halves of the exuviae which cling to the leaf following the ecdysis. The hatching process lasts from 2 to 5 minutes.

Colour of T. althaeae

Before discussing the questions connected with colouring, it is necessary to mention the method adopted for my own investigations. These were carried out on two populations which according to their origin will be referred to herein-after as the "Höfchen population" and the "Hallertau population". To a certain extent, differences in colour were established between both populations which can best be expressed by comparing them.

Stage	Hallertau population	Höfchen population
Summer females	green to green-brown	carmine red to dark red
Winter females	orange to brick red	not observed

All the other stages of both populations resemble each other in colour. The freshly laid eggs are as clear as glass; during the course of the embryonal development they assume a yellowish colour, and shortly before hatching they have an opalescent glitter.

All active stages are coloured green in normal cases, and the stomach blind sacs appear as dark spots on the sides of the body. The colour of the chrysalis stages changes from green to green-yellow and finally to a deep yellow. This colour is given a silvery gloss by the air trapped between the old integument and the new nymph skin. The colour of the males of both populations varies between bright green and ochre-yellow.

The colours just described may be seen in normal cases, although colour changes may be caused as a result of changes in the feeding conditions. It was often perceived that the nymph stages on yellow, chlorotic leaves revealed a yellow colour similar to that of the leaves. This colour, however, changed back to the normal green after sucking for four to six hours on healthy green leaves. All stages present on red hop leaves in late Autumn had a reddish colour. Reference to the investigations of Reiff (1949) on the connection between leaf metabolism and the colour of the mites will be made in the section on "Hibernation".

The described differences in colour of the summer females of both populations are, however, fixed genetically and cannot be influenced by external factors. Because both types react in more or less the same manner to varying relative humidity and other ecological factors with respect to their development and oviposition and moreover have a well-pronounced spinning capacity characteristic of *T. althaeae*, and also have the same plant hosts, it is assumed that despite these colour differences they are one and the same species. Similar observations were made with *T. althaeae* (*T. bimaculatus* Harvey) in America (Neiswander 1950) where the two varieties, which reveal no morphological differences whatsoever, are referred to as the "green type" and the "red colour type".

IV. Geographical propagation and host plants of *T. althaeae*

In view of its wide propagation, *T. althaeae* may be referred to as being cosmopolitan. As a plant pest, it plays a part both in the temperate zones as well as in the tropics. It is found outdoors in practically all European countries, although in Sweden (Traegardh 1915) it is only known to occur in greenhouses. Outside Europe its appearance has been established in North America, Turkey, Egypt, Java, Sumatra, the Philippines and Guayana. According to this, the reaction type of *T. althaeae* is not subject to specific climatic conditions.

The wide area of propagation is closely related to the large number of plants this insect has as hosts. It is known that in North America alone there are 183 different types of plant hosts, and Zacher (1920) established 150 in Germany.

Disregarding data given in pertinent literature, and in fact to supplement these, I arranged investigations to ascertain the range of plant hosts. The plants under investigation were placed in a greenhouse and colonized with females of *T. althaeae*, and the oviposition and development observed. Particular attention was paid to the weeds occurring in fields because these may play an important part as possible intermediate hosts in the epidemiological behaviour of *T. althaeae* (Grob 1951, Chapman and Lienk 1950, Wilhelm 1951). The following plant types and varieties revealed themselves to be suitable as hosts for *T. althaeae*:

Hops	<i>Humulus lupulus</i>
Kidney bean	<i>Phaseolus vulgaris</i>
Cucumber	<i>Cucumis sativus</i>
Pumpkin	<i>Cucurbita pepo</i>
Potato	<i>Solanum tuberosum</i>
Tomato	<i>Solanum lycopersicum</i>
Garden beet	<i>Beta vulgaris crassa</i>
Sugar beet	<i>Beta vulgaris saccharifera</i>
Rape	<i>Brassica napus oleifera</i>
Broad bean	<i>Vicia faba</i>
Spinach	<i>Spinacea oleracea</i>
White clover	<i>Trifolium repens</i>
Red clover	<i>Trifolium pratense</i>
Alfalfa	<i>Medicago sativa</i>
Yellow clover	<i>Medicago lupulina</i>
Apple	<i>Pirus malus</i>
Pear	<i>Pirus communis</i>
Plum	<i>Prunus domestica</i>
Sweet-cherry	<i>Prunus avium</i>
Peach	<i>Prunus persica</i>
Greengage	<i>Prunus insitica</i>
Vine	<i>Vitis vinifera</i>
Rose	<i>Rosa sp.</i>
Strawberry	<i>Fragaria sp.</i>
Carnation	<i>Dianthus sp.</i>
Violet	<i>Viola sp.</i>
Dahlia	<i>Dahlia sp.</i>
Ox-eye daisy	<i>Chrysanthemum leucanthemum</i>
Elder	<i>Sambucus sp.</i>
Stinging nettle	<i>Urtica dioica</i>

Red dead nettle	<i>Lamium purpureum</i>
White dead nettle	<i>Lamium album</i>
Henbit	<i>Lamium amplexicaule</i>
Hemp-nettle	<i>Galeopsis tetrahit</i>
Groundsel	<i>Senecio vulgaris</i>
Ivy-leaved speedwell	<i>Veronica hederifolia</i>
Charlock	<i>Sinapis arvensis</i>
Wild radish	<i>Raphanus raphanistrum</i>
Lamb's-quarters	<i>Artiplex</i> sp.
Sorrel	<i>Rumex acetosa</i>
Curled dock	<i>Rumex crispus</i>
Bush vetch	<i>Vicia sepium</i>
Tufted vetch	<i>Vicia cracca</i>
Common chickweed	<i>Stellaria media</i>
Bishop's weed	<i>Aegopodium podagraria</i>
Galinsoga	<i>Galingsoga parviflora</i>
Lesser bindweed	<i>Convolvulus arvensis</i>
Common hawkbit	<i>Leontodon hispidus</i>
Dandelion	<i>Taraxacum officinale</i>
Broad leaved plantain	<i>Plantago major</i>
Hoary plantain	<i>Plantago media</i>
Ribwort plantain	<i>Plantago lanceolata</i>
Hawkweed	<i>Hieracium</i> sp.

Even though it cannot be claimed that these investigations on the range of plant hosts are comprehensive, they nevertheless characterize *T. althaeae* as a polyphagous parasite. The economic significance of this will be dealt with in greater detail in the next chapter.

V. Economic significance of *Tetranychus althaeae*, damage caused and its appearance

Among the family of Tetranychidae which consists of a large number of plant parasites, *T. althaeae* is in view of its polyphagia and large-scale propagation undoubtedly the most important from an economical point of view (Zacher 1921). Under European, and in particular German conditions, this pest inflicts considerable damage to ornamental plants, cucumbers etc. (Fleischmann 1951) growing in nurseries and greenhouses. Recently it has also gained a footing as a parasite on fruit trees (Grob 1951) where as a result of its fast rate of reproduction it has partly suppressed *Paratetranychus pilosus* C. and F. and *Bryobia praetiosa* Koch. Moreover, it is often mentioned as a pest occurring in viticulture (Wilhelm 1951), and in the last few years its epidemic occurrence on potatoes in Thüringen (Seiffert 1951) has led to heavy damage and economical losses. Its greatest role, however, is played as a pest occurring almost regularly on hops in all hop growing countries throughout the world (Hamp 1936, Linke 1950, Jary 1935). It is not possible to give any general and reliable details on the extent of the damage inflicted in this field, because this depends upon the degree of infestation and its propagation in relationship to the ecological factors, and upon the success of the control measures etc. The significance the loss it causes may assume is shown in the following comparison of yields per hectare (2.47 acres) obtained in 1933, 1934 and 1935 in Hallertau. While 1420 kg and 1525 kg per hectare were harvested in

1933 and 1935 respectively, the yield per hectare in 1934, a year in which mites predominated, amounted to only 755 kg. In heavily infested gardens, yield losses of up to 70 % and 80 % are not a rarity, and in 1950 several growers reported complete crop failures as the result of spider mite infestations. The damage caused by *T. althaeae* also has its effect in the following year because only little or no reserve nutrition can be produced from the injured leaves or from those which died prematurely. This nutrition should be stored in the roots and is intended to serve as the first food for the vines in the following year.

The decrease in the value of the hop cones caused by the so-called "Kupferbrand" (copper stain) resulting from the infestation of the common spider mite is just as worthy of consideration as the quantitative loss. This decrease in value is all the more important since it not only appears outwardly but also leads to a reduction of the bitter element content determining the brewing value. According to investigations made by Zattler (1950), the most important ingredient of the bitter element, the alpha acid, and the bitter element contents were found to be approximately 14 % and 12 % lower respectively for a hop infested with copper stain when compared with healthy cones.

T. althaeae pierces the plant tissues with its stylet-like mandibles chiefly on the lower surface of the leaves, and because it can only take liquid nourishment due to the anatomical peculiarities of the digestive system it sucks out a part of the cell contents. Investigations by K u e n e n (1946) on *P. pilosus* and G ü n - t h a r t (1945) have shown that the chlorophyll is partly dissolved and destroyed by enzymes of the secretion from the salivary glands. Corresponding investigations for *T. althaeae* have not been made although it appears justifiable to take over the results obtained with *P. pilosus* particularly as R e i f f (1949) was able to prove with *T. urticae* that pigment parts of the chloroplasts are also stored in the mid-intestine and in the storage organ.

As a result of cell necrosis and the withdrawal of chlorophyll, the infection spots caused by the sucking activity of *T. althaeae* change in colour after a short time from a yellowish tint to the typical pale yellowish-brown colour which is the reason why German hop growers call this disease "Kupferbrand" (copper stain). The infection spots are never distinctly outlined but are always shaped irregularly. As they provide a striking contrast to the dark green of the upper surfaces of the leaves, they appear much more clearly on these surfaces than on the lower surfaces. They can be recognized particularly well in transmitted light.

When the infestation is heavy, the single spots flow into each other so that the whole leaf assumes a copper colour.

Necrosis is followed by post-mortal processes. These are made manifest by the leaves drying up and shedding at a later date (Fig. 3). It is not difficult to diagnose satisfactorily because even slight sicknesses provide specific disease appearances and the easily visible parasite itself magnified tenfold represents a clear symptom. Furthermore the web spun by *T. althaeae*, which may assume considerable proportions and can under certain circumstances cover the whole leaf, is clearly perceptible, and indicates beyond all doubt an infestation by spider mites.

In years of mass reproduction, infestation by *T. althaeae* also spreads to the cones where the pests not only find suitable conditions for obtaining food but also acceptable protection against wind, rain and dew. The manner in which the symptoms reveal themselves differs dependent upon the time of the infesta-

tion and the development stage of the cones. When the infestation occurs very early the cones do not close, the cone leaves grow wide apart and are copper red. The lupulin is no longer gold-yellow, but is coloured brown and there is less of it because the formation of the lupulin glands is inhibited by the early infestation. When the cones are infested at a later date they grow to their full size and are also closed but they have a peculiar yellow-red tint. If in such cases an emergency harvest is not arranged in good time, the cones change to a red-brown colour and dry up. Even a small percentage of such discoloured cones has an unfavourable effect economically because under certain circumstances it may spoil the otherwise good all-round impression of a whole crop. Mention has already been made of the reduction in quality that is involved.



Fig. 2. Healthy hop plantation (Orig.)



Fig. 3. Hop plantation seriously damaged by spider mites (Orig.)

The symptoms of infestation on leaves and cones so far described do not appear uniformly and simultaneously on the whole hop plant but are first seen on the lower parts according to the course of the infestation, becoming perceptible on the upper plant parts as the mites gradually migrate in an upward direction.

The damage caused by the sucking activities of *T. althaeae*, involving a decrease of the assimilation surface and an increase of evaporation (Gasser 1951, Günthart 1945), finally results in a weak formation of the complete vegetative apparatus including the cones, and of course a much lower yield. This is made particularly apparent when comparing a healthy hop plantation and a plantation seriously damaged by *T. althaeae* (Figs. 2 and 3).

VI. Investigations on the biology of *Tetranychus althaeae*

The central point of all the investigations was the question about the influence of abiotic factors on the biological behaviour of *T. althaeae*. In view of this, greater importance was attached to the observations and experiments outdoors, and experiments in the laboratory were only carried out to supplement and clarify special parts of questions.

A. Post-embryonic development

The experiments on the post-embryonic development were intended to ascertain the period of development at various temperatures, namely

1. under outdoor conditions,
2. under set conditions.

1. Post-embryonic development under outdoor conditions

a) Method

The clarification of biological questions concerning whole populations is quite a difficult matter and conceals sources of error which can only be eliminated to an unsatisfactory degree or in fact not at all, and in view of this an attempt was made to obtain an insight into the biological behaviour of *T. althaeae* by observing isolated individuals. The investigations carried out by Andersen (1948) on *Paratetranychus pilosus* C. and F. have proved that it is possible to work in this direction even with relatively small mites. Therefore the single isolations were carried out on the same lines as those described in Anderson's method. *Phaseolus vulgaris* and *Humulus lupulus* were used as plant hosts. In order to acquire conditions approaching those in nature, the potted plants were placed on a work bench outdoors. *Phaseolus vulgaris* were used as a host solely in a primary leaf stage, and from *Humulus lupulus* lateral sprouts approximately 30 cm long with roots were taken. Both plant hosts were renewed regularly at intervals of 8 to 10 days.

The work site was surrounded with strengthened mull to eliminate the effects of strong winds without completely preventing ventilation. The disturbing effect of heavy rainfall during the observations was also eliminated whenever necessary by setting up a temporary roofing of garden frames.

The individuals to be observed were caught under the binocular lens by means of a fine dissecting needle, and transferred to single, marked leaves of the potted plants. Their development was registered by checking them twice daily. During the vegetation period in 1951, four freshly hatched larvae were isolated per leaf of the plant hosts in this manner from May 21 until the end of October in order to obtain exact data on the period of development of *T. althaeae* with respect to all possible temperature values and the various average temperatures thus obtained.

A vaseline ring was applied to the leaf stalks to prevent the mites from migrating from the leaves.

Thermohygrographs were set up in the immediate vicinity of the individual isolations to register more or less exactly the temperature and relative humidity. By arranging the experiment and recording the temperatures in this manner, any differences between the climatic conditions of a large area and the climate prevailing in a stock which arise in a densely cultivated stock are eliminated. It may be assumed with certainty that the stock climate plays an important part

particularly in hop growing, although its influence increases as the size and density of the plants increase (Geiger 1950). Unfortunately there are no exact measurements of this type available for hop growing, and in fact they could only be carried out by using complicated and expensive equipment.

b) Implementation

The investigations were carried out on two populations. The one originated from the greenhouse of the experimental farm at Höfchen where it chiefly occurs on *Phaseolus vulgaris* and the other population was from the Bavarian hop growing district, the Hallertau (see Morphology). Both populations were identical to such a considerable degree with respect to development and egg laying that it was not necessary to compile two separate sets of results. The temperatures given are mean values. The single mean daily temperatures, used as the basis for calculating the all-round average temperatures, were calculated from six single values recorded in each case by the thermohygrographs. It was decided not to reproduce the corresponding moisture values seeing that the relative humidity fluctuated between 55 and 100 % under outdoor conditions, and its influence was of no practical significance as long as there were no extreme conditions prevailing over a long period of time (Bodenheimer 1926, Uvarov 1930). (Mention will be made to the influence of high relative humidity prevailing for a long period in the discussion on the laboratory investigations).

All the values are based on observations made with females, and the period of development was taken from the time the larvae hatched until the appearance of the imago.

The mean error of the average value was calculated according to the commonly used formula

$$m = \pm \sqrt{\frac{\sum V^2}{n \cdot n - 1}}$$

c) Result

The results of 133 single observations, in which the dependence of the post-embryonic development period upon the temperature was ascertained for 10 different average temperatures, are clearly given in Table 1.

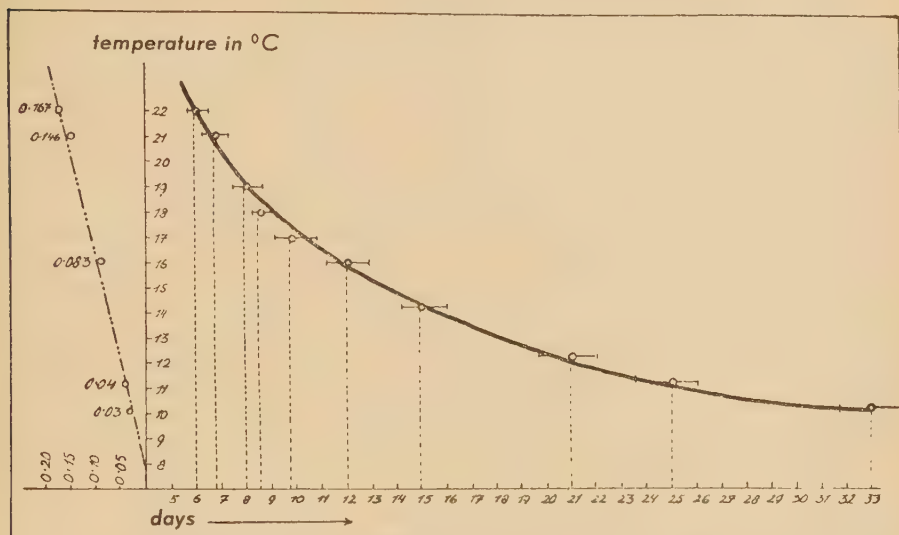
Table 1

Temperature in °C	Development period expressed in days mean error	Number of Observations
22.0 ± 0.3	6.0 ± 0.09	12
21.0 ± 0.3	6.8 ± 0.07	14
19.0 ± 0.5	8.0 ± 0.15	14
18.0 ± 0.3	8.5 ± 0.11	13
17.0 ± 0.3	9.8 ± 0.11	10
16.0 ± 0.5	12.0 ± 0.12	14
14.3 ± 0.4	15.0 ± 0.11	15
12.2 ± 0.2	21.0 ± 0.14	16
11.1 ± 0.3	25.0 ± 0.14	14
10.1 ± 0.4	33.0 ± 0.22	11

The following graph (Graph I), in which the abscissa gives the development period and the ordinate the respective temperature, provides the basis for the above values. The development period reveals considerable individual differences.

The extent of variation observed in each case may be seen from the intersections between the dotted lines and the curve.

Graph 1



The progress of the curve reveals the decisive influence of the temperature on the period of the post-embryonic development of *T. althaeae*. Any increase in temperature within the temperature range of 10.1°C and 22°C leads to a shortening of the post-embryonic development.

d) Period of single stages dependent upon the temperature

Whereas Graph 1 only shows the total period of development dependent upon the temperature, it would appear expedient, particularly in view of the prognostic usability of the material, to reproduce the period of the individual stages in relation to the temperature. The results given in the following table are once again average values.

Table 2

Temp.	L.	Nchr.	PrN.	Dchr.	DN.	Tchr.	C.T.
10.0	6.0 (14)	4.8 (12)	4.0 (11)	4.5 (10)	5.5 (13)	6.0 (12)	30.8
12.2	4.0 (15)	3.3 (11)	3.0 (11)	3.4 (13)	4.0 (13)	4.0 (10)	21.7
14.3	3.0 (12)	2.7 (11)	2.0 (14)	2.6 (13)	2.8 (12)	2.5 (10)	15.6
16.0	2.5 (13)	2.0 (10)	1.6 (12)	2.0 (14)	2.3 (12)	2.0 (13)	12.4
18.0	2.0 (11)	1.5 (14)	1.2 (13)	1.3 (11)	1.6 (12)	1.6 (10)	9.2
22.0	1.5 (12)	1.0 (14)	0.8 (12)	1.0 (12)	1.0 (14)	1.0 (11)	6.3

Key to Table 2:

L. = larva
 Nchr. = nymphochrysalis
 PrN. = protonymph
 Dchr. = deutochrysalis
 DN. = deutonymph
 Tchr. = teliochrysalis
 C.T. = cross totals

Figures without brackets: period of the respective stage expressed in days
 Figures in brackets: number of observations

The results show that the relationship between each stage of the post-embryonic development and the temperature is the same as that for the post-embryonic development as a whole. It was established beyond all doubt that the larval stage was the longest and the protonymph stage was the shortest, while in the other stages it was not always possible to establish definite differences. The fact that the cross total of the individual values does not fully correspond in all cases with the total development period corresponding to the respective temperature (see Graph 1) may be due to the following reasons:

1. the shortness of the development period in the individual stages and the inexactitude thus caused;
2. unavoidable lack of experimental method; the check on the outdoor isolations carried out twice daily rendered possible, at the best, an exactitude to one half day.

e) Shortening of male development

The regular early appearance of the *T. althaeae* male which was observed has always been explained by the absence of a deutonymph stage in the male's life-cycle. This standpoint can be disputed on the basis of numerous individual observations which reveal that the epimorphosis of the male does not differ fundamentally from that of the female. The earlier appearance of the male is caused by the short life-cycle which may be explained chiefly by a shortening of the deutonymph stage. Andersen (1948), who made the same observations with *Paratetranychus pilosus* C. and F. assumes that the reason for this is the greater need for nourishment on the part of the female deutonymph which, particularly in this stage, grows very quickly in comparison with the male deutonymph.

Several values obtained at different average temperatures have been taken from the number of individual observations carried out in this connection to illustrate the point under discussion and are compared with each other in Table 3 which also expresses the degree of shortening as a percentage.

Table 3

Temperature in °C	Development Period in days		Shortening in the male sex expressed in %
	Female	Male	
20.8	7	6.2	7.2
18.8	8	7.2	10.0
17.2	10	8.9	11.0
16.1	12	10.5	12.5
15.3	13	11.8	9.3
13.5	16	14.5	9.4
12.4	20	18.0	10.0
10.3	29	26.0	10.7

The shortening of development in the male sex ascertained from 32 individual observations amounted to 10.2 %.

2. Post-embryonic development under set conditions

Even though the outdoor investigations clearly showed that all vital functions of *T. althaeae* are dependent upon temperature, it appeared advisable also

to carry out experiments in this connection at constant temperatures in the laboratory to ascertain to what extent values obtained under set conditions can be utilized outdoors.

a) Investigation of the period of development at constant temperatures and constant relative humidity

aa) Method

The experiments were carried out in the laboratory at $18^{\circ} \pm 0.8$, $22^{\circ} \pm 0.8$ and $25^{\circ} \text{C} \pm 1$. The first two temperatures were kept constant in the laboratory allowing for the given deviation, whereas $25^{\circ} \pm 1$ was the temperature used in the insect breeding room at the Experimental Farm in Höfchen.

In order to obtain comparable values, it was deemed advisable to keep the relative humidity constant for the period of the experiment. Therefore they were carried out under five litre capacity bell jars in which the relative humidity of 70 %* chosen to represent the experiment condition was attained by placing a Petri dish containing 44 % sulphuric acid (% per weight) in the jar. To keep any deviations occurring at a minimum, potted plants were not used but instead single bean shoots set in glass bottles containing nutrient solution. The bottle necks were closed by placing a strip of cellulose around the plant stem.

The temperature and humidity were checked by means of a hair hygrometer with thermometer placed in the bell jar. The airing of the bell jar resulting from the check made twice daily prevented any concentration of CO_2 . The larvae were isolated in accordance with the method already described (Page 193).

bb) Result

The result of the experiment is given in Table 4. In Tables 4 and 5 the values ascertained at constant temperatures and the corresponding mean temperatures under outdoor conditions are reproduced for comparison.

Table 4

Constant temperature	Development period expressed in days mean error	No. of observations
18.0 ± 0.8	9.5 ± 0.16	11
22.0 ± 0.8	7.5 ± 0.15	12
25.0 ± 1.0	6.3 ± 0.18	14

Table 5

Mean temperature	Development period expressed in days mean error	No. of observations
18.0 ± 0.3	8.5 ± 0.1	14
22.0 ± 0.3	6.0 ± 0.07	14
25.0	not observed outdoors	

On comparing tables 4 and 5 it is evident that an acceleration in development occurred outdoors at the corresponding average temperatures.

* This value was calculated empirically, because it was found in preliminary tests that the data given in literature (Z w ö l f e r 1932) on water vapour pressure with various H_2SO_4 concentrations do not apply for experiments with living plant stock.

b) *Investigations of the period of development at fluctuating relative humidity and different temperatures*

The purpose of the investigations was to determine the influence of different degrees of relative humidity on the course and the period of the post-embryonic development.

aa) Method

The relative humidity was regulated by placing salts, sulphuric acid and water in the bell jars.

The following values were obtained:

55 % relative humidity with $\text{Ca}(\text{NO}_3)_2^*$

70 % relative humidity with H_2SO_4 44 % (% per weight)

100 % relative humidity with H_2O .

The salts and the sulphuric acid were renewed whenever required. The temperatures of 22° and 25°C selected to represent the experiment conditions were kept constant in the laboratory and the insect breeding room making allowances for the given deviations. The course of development was checked by observing the insects twice daily under the binocular lens, and the development stage registered each time was entered in the experiment log book.

bb) Result

The results of the investigations are compiled in Table 6.

Table 6

Relative humidity	$22^\circ\text{C} \pm 0.8$		$25^\circ\text{C} \pm 1.0$	
	Period of development expressed in days mean error	number of observations	Period of development expressed in days mean error	Number of observations
100 %	8.6 ± 0.20	15	7.3 ± 0.07	15
70 %	7.5 ± 0.15	12	6.3 ± 0.18	14
55 %	7.4 ± 0.18	14	6.3 ± 0.20	12

It is of particular interest that in 30 % of all the observed cases a full development to the imago stage did not result at 22°C and 100 % relative humidity.

c) *Tests on the effect of extremely high relative humidity*

The result of the experiments described under b) gave rise to the investigations described below which dealt specially with the effect of extremely high relative humidity on the post-embryonic development of *T. althaeae*.

aa) Method

The experiments were carried out in the laboratory under bell jars at temperatures of $22^\circ\text{C} \pm 0.8$, $18^\circ\text{C} \pm 0.8$ and $14.5^\circ\text{C} \pm 0.3$. The relative humidity in each case was 100 %. In order to obtain conditions similar to those prevailing

* $\text{Ca}(\text{NO}_3)_2$ first became effective in the manner desired after it had been rendered completely free from water by evaporation.

outdoors during long periods of rain, the lower surfaces of the leaves were wetted daily.

bb) Result

The results may be summarized as follows: Over a long period of time, the effect of persisting 100 % relative humidity in combination with liquid water on the lower surface of the leaves was strongly inhibitive on the post-embryonic development of *T. althaeae*, and in fact this effect increased as the prevailing temperatures decreased.

At 22°C the development ended on an average after 7 days with the death of the protonymph, at 18°C the development ended the same way after 8 days, and at 14.5°C all the larvae died after 3 to 4 days.

Summary and discussion of results

All the investigations confirm that the rate of development is dependent upon temperature, which was to be expected with spider mites seeing that they are poikilothermic animals.

The following results were obtained in the outdoor tests carried out to investigate the post-embryonic development of *T. althaeae*.

1. The values obtained outdoors with respect to the period of post-embryonic development clearly show when reproduced as a graph that when the temperature increases the rate of development also increases. The shortest period of development calculated from the hatching of the larva to the imago was found to be 6 days at 22°C, while the longest was 32 days at 10.1°C.

The development optimum, which according to Vasseur (1938) is supposed to be between 29° and 31°C, could not be obtained in these investigations because the average temperatures prevailing in 1951 were not high enough for a sufficiently long period.

The zero point of development, determined mathematically by construction of the reciprocals of the development period (Stellwaag 1944), occurs at 7.7°C. This value coincides with the observations made outdoors, according to which both egg laying as well as the development of *T. althaeae* ceased at temperatures between 7.5°C and 8.5°C. This would seem to prove that the assumption of Vasseur (1938) that the zero point of development for *T. althaeae* is between 10° and 12°C does not apply generally.

2. The single stages of post-embryonic development show the same relationship to temperature as does the post-embryonic development on the whole. At the same temperatures, the larval stage proved to be the longest whereas the protonymph stage was the shortest.
3. The reason for the shorter period of development of the males is not the absence of a stage but the shorter deutonymph stage in the epimorphosis of the male sex.

The results obtained in the laboratory experiments on the period of post-embryonic development were as follow:

1. The values obtained for the post-embryonic period under constant temperatures do not coincide with the corresponding average temperatures obtained outdoors where a definite acceleration of development was observed regularly. (Stellwaag [1944] made similar observations in his investigations carried out on *Clysia ambiguella* and *Polychrosis botrana*).

The reasons for the differences occurring in the period of development have not been clarified. It is, however, quite evident beyond all doubt, that an individual taken away from its natural surroundings behaves quite differently under the set conditions of laboratory experiments from the way it behaves under the ever changing conditions outdoors. It could be imagined that the acceleration of development outdoors caused by rising temperature fluctuations is greater than the delay in development caused by corresponding falling temperature fluctuations. Possibly a certain part is also played by the different kinds of conditions outdoors with respect to the light factor and the gas exchange influenced by air movement.

It appears justified to conclude that as a result of the discrepancy between results obtained outdoors and those obtained in the laboratory, the latter can only be used as a prognostic aid with limitations, and it would be a mistake to apply the results of laboratory and thermostat tests of this nature carried out with *T. althaeae* to outdoor conditions.

2. The period of the post-embryonic development of *T. althaeae* was influenced by varying relative humidity. High and constant relative humidity in the laboratory tests resulted in a perceptible delay in development. It would not appear justified to apply these results to outdoor conditions under which the relative humidity — apart from extreme cases — always fluctuated between 55 and 100 %. Just the same the results show that optimal conditions for the development of *T. althaeae* are below 70 % relative humidity. The old experience that besides heat, dry conditions are also required for the mass development of *T. althaeae* is thus confirmed.
3. When liquid water was present on the lower surface of leaves of the plant hosts the post-embryonic development of *T. althaeae* came to an earlier end in the form of death as the prevailing temperatures decreased.

When examined epidemiologically the experiment results may be evaluated as follows:

1. Constant warm weather results in an increase of the number of generations and accordingly the density of the population.
2. The more rapid development of *T. althaeae* at high temperatures results in an intensification of the sucking activities thus increasing the damage inflicted.
3. Long periods of rainy weather inhibit the development and gradation, particularly at low temperatures. The result of the historical-statistical investigations carried out by Zattler (1936), who deduced from these that the weather in May is of prognostic significance, is clearly explained by the experiments on the effect of extremely high and persisting relative humidity described on Page 198.

B. The embryonic development

The purpose of the investigations was to ascertain the period of embryonic development, in other words the development of the individuals from the time the egg is laid, until the larva emerges, namely

1. under outdoor conditions,
2. under set conditions.

1. Embryonic development under outdoor conditions

a) Method

The method adopted for this experiment (recording of temperature and relative humidity, plant hosts used etc.) was the same as that for the "Investigations of the post-embryonic development" described on Pages 193 and 194.

b) Implementation

The egg laying of isolated females (see method for "Investigations of oviposition", Page 204) was recorded on the sketch of a leaf (Fig. 4). The hatching dates were determined by checking the eggs twice daily under the binocular lens.

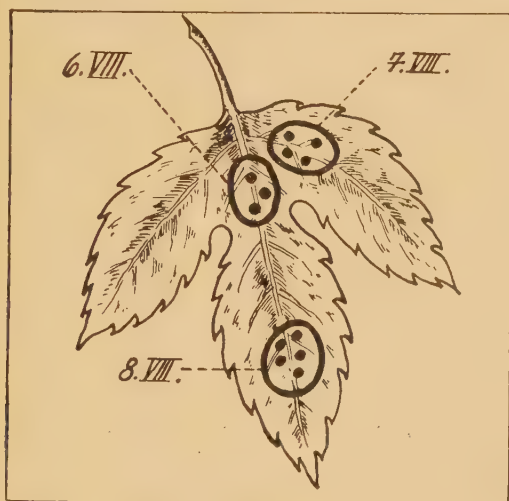


Fig. 4. Sketch of a hop leaf with the laid eggs marked by dots

c) Result

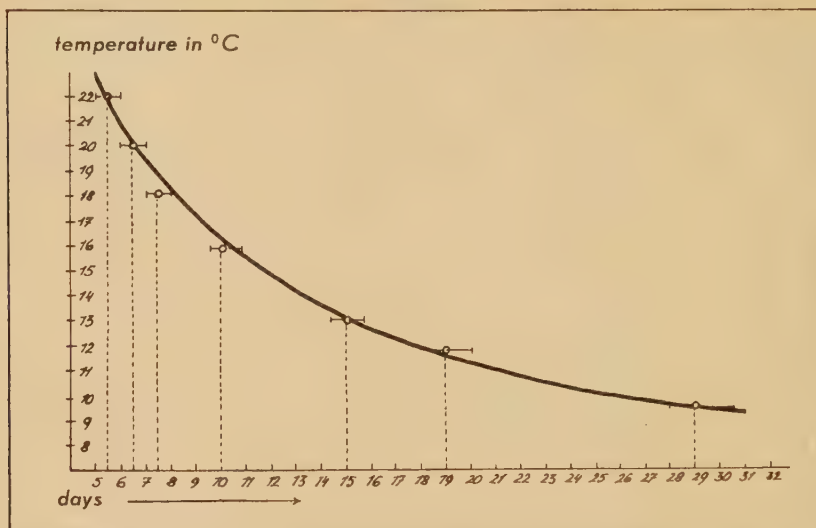
The results of 86 individual observations made in all, in which the dependence of the embryonic development period upon the temperature was ascertained for 7 different average temperatures, are given in the following table (Table 7):

Table 7

Temperature in °C	Period of development expressed in days mean error	Number of observations
22.0 ± 0.3	5.5 ± 0.11	14
22.0 ± 0.3	6.5 ± 0.12	13
18.0 ± 0.3	7.4 ± 0.09	12
15.9 ± 0.5	10.0 ± 0.11	12
13.0 ± 0.4	15.0 ± 0.11	15
11.9 ± 0.4	19.0 ± 0.15	10
9.8 ± 0.5	29.0 ± 0.18	10

The following picture is obtained when these values are reproduced as a graph.

Graph 2



The course of the curve shows the decisive influence the temperature has on the period of embryonic development of *T. althaeae*.

2. Embryonic development under set conditions

a) Investigations of the length of the embryonic development at constant temperatures and constant relative humidity

The purpose of these experiments was to clarify the question whether the values for the period of embryonic development obtained in the laboratory at constant temperatures coincide with those obtained at corresponding average temperatures outdoors.

aa) Method

The experiments were carried out under the same conditions as those prevailing for the investigations on "Post-embryonic development under set conditions". Detailed information is given on Pages 196 and 197.

Females were transferred to the plants under the bell jars. Egg laying was registered on sketches of the leaf, and the time when the larvae emerged was ascertained by checks carried out twice daily.

bb) Result

The developing times obtained under constant temperatures and the corresponding values for outdoor conditions are reproduced in Tables 8 and 9.

Table 8

Constant temperature outdoors	Period of development expressed in days mean error	Number of observations
18.0 ± 0.8	8.5 ± 0.12	16
22.0 ± 0.8	6.8 ± 0.16	9
25.0 ± 1.0	4.2 ± 0.14	9

Table 9

Average temperature outdoors	Period of development expressed in days mean error	Number of observations
18.0 ± 0.3	7.3 ± 0.11	10
22.0 ± 0.3	5.5 ± 0.11	17
25.0	not observed outdoors	

On comparing Tables 8 and 9, it is clearly seen that the development period at constant temperatures is extended.

b) *Investigations of the period of the embryonic development at fluctuating relative humidity and different temperatures*

The following experiments were carried out to clarify the question whether, and to what extent, the embryonic development of *T. althaeae* is influenced by fluctuating relative humidity.

aa) Method

The tests were arranged analogous to the investigations described on Page 198 with respect to the influence of various degrees of relative humidity on the post-embryonic development.

bb) Result

The results of the experiments are reproduced in Table 10.

Table 10

Relative humidity	22° C ± 0.8		25° C ± 1.0	
	Period of development expressed in days	Number of observations	Period of development expressed in days	Number of observations
100 %	6.8 ± 0.14	14	4.3 ± 0.1	14
70 %	6.8 ± 0.16	8	4.2 ± 0.14	9
55 %	6.8 ± 0.19	14	4.2 ± 0.18	12

Summary and discussion of results

The following points were established in the outdoor investigations carried out to determine the period of embryonic development:

1. The decisive influence of the temperature on the period of embryonic development is clearly expressed in the graph (Graph 2) which is very similar to that for the post-embryonic development. Increases in temperature within the temperature range of 9.8° and 22° C mean a shortening of the embryonic development. The shortest period of development was 5.5 days registered at 22° C, whereas the longest was 29 days at 9.8° C.
2. There is a relationship between the period of post-embryonic development and that of the embryonic development, namely at the same temperatures outdoors as follows: Calculated as the average of all observations, the period of the embryonic development amounted to 83 to 86 % of the post-embryonic.

The following results were obtained from the laboratory experiments carried out to determine the period of embryonic development:

1. The values for the period of embryonic development obtained in the laboratory at constant temperatures do not agree with those obtained at corresponding average temperatures outdoors. The period of development was accelerated under varying outdoor conditions. Reference has already been made to the suppositions concerning the causes of this development acceleration in the discussion on the investigations of post-embryonic development on Page 199.
2. The influence of fluctuating relative humidity on the period of embryonic development of *T. althaeae* is so slight that practically no use can be made of it. It is concluded from this that the vital optimum of the egg stage lies within wide limits with respect to the relative humidity.

C. Investigations of oviposition under outdoor conditions

1. Method

Details concerning the arrangement of the experiments, such as the type and the development stage of the plant hosts, recording of temperature and relative humidity, method of isolation etc. are given on Pages 193 and 194 (Method for "Investigations of post-embryonic development").

2. Implementation

Beginning on May 21, two freshly hatched females were isolated in each case on single leaves of the plant hosts at intervals of two days. Their egg laying was followed by daily checks. In order to simplify the counting of the eggs freshly laid each day, the females were transferred regularly to fresh plants at intervals of 3 to 4 days.

3. General comments on oviposition

The fertilization takes place in most cases before the egg laying. The males, always ready to fertilize, often wait in groups in the immediate vicinity of the female *Teliochrysalis* stages for the young females to emerge which are then immediately puberal. The copulation often begins before the young female has completely freed itself from the old nymph skin. The position of copulation conforms with that observed by Andersen (1948) for *Paratetranychus pilosus* C. and F. It can be termed as a head stand with the male underneath the female and moving its pointed abdomen upwards and forwards until it meets the genital orifice of the female. The period of the sexual union varies between 1.5 and 7 minutes. It was often observed that freshly fertilized females were fertilized a second and a third time by other males immediately after the first copulation. Generally the old females resist the ready-to-fertilize males, although it was observed that they also submitted to a further copulation in several cases.

The fertilization of female deutonymphs, as described by Gasser (1951), was never observed.

Between the fertilization and the egg laying is the preovipositional period which lasted 1 to 6 days, the average calculated from all the observations amounting to 2.4 days. It is during this preovipositional period that the females begin to spin the webs. (Of the Tetranychidae, *T. althaeae* has the greatest spinning capacity; even its juvenile stages are capable of spinning although to a much lesser degree than the females.) The purpose of the web is to protect

above all the juvenile stages from being wetted by rain and being blown away by the wind. In this connection, mention should be made of the urgent importance of destroying this web during the control by careful spraying, applying corresponding pressure in order to ensure that the mites are properly wetted with the acaricide used.

4. Location of oviposition

In 97 % of all the cases observed, the eggs laid were distributed at irregular intervals over the complete lower surfaces of the leaves. In certain experiments the side shoots of hops were placed in such a position that the lower leaf surfaces covered with spider mites were facing upwards with the result that within 4 to 8 hours the mites all reacted by emigrating to the upper surfaces which in these particular instances were facing downwards. There were in fact individual cases of normal egg laying and development taking place on these upper surfaces. The reason for the spider mites taking to the lower surfaces is not, however, due to a desire to avoid direct sunlight but may be attributed to an instinctive aspiration to find better protection against rain, wind and other external influences. Regarding the localization on the entire plant, the outdoor observations made on hops — in agreement with those made again and again in the field — showed that the infestation, or rather the egg laying, begins on the lower parts of the plants and gradually makes its way upwards. It was also established that only females take part in these movements to the upper parts of the plants in order first of all to seek better feeding conditions for themselves and secondly, by instinct, to ensure that the newly-hatched larvae are provided with favourable feeding conditions during their juvenile development. The speed of this upward migration depends upon the density of the infestation.

Any connection between the age of leaves and preference shown with respect to the site of egg laying was not established; the old leaves of the main shoots were infested just as much as the newly grown leaves of the side shoots.

The eggs appear to be firmly attached to the leaves by means of a secretion which surrounds the egg at the time it is laid and then dries later. It is only with difficulty that the eggs can be removed from the leaf with a dissecting needle; the immersion of whole leaves in water did not result in the loss of any eggs. It was often observed — particularly where there was a heavy infestation — that the eggs were laid direct in the web.

5. Number of eggs

On working out the average of 125 individual observations, it was found that a female of *T. althaeae* laid a total of 94 eggs. This is confirmed by G a r l i c k (1929) who counted 90 eggs on raspberries, while the figures given by other authors vary to a considerable extent.

The maximum per female was 128 eggs and the minimum 73. The maximum number of eggs laid per day was 15 at 21°C, whereas the minimum was one egg at 9.4°C. The fluctuations in the daily laying of eggs are very great. This is made clearer by the following observations:

1. It is evident from all the observations made that there is a certain periodicity with respect to the number of eggs within the entire period of egg laying. It was seen that the number of eggs laid daily at the beginning of the egg laying period was rather low, increasing towards the middle of this period only to drop again towards the end.

2. The prevailing temperature definitely has an influence. Even though it is difficult due to the relatively great fluctuations in temperature during the entire period of egg laying to arrive at any specific laws in this connection, some of the individual observations described below do show that the laying of eggs is dependent upon temperature. The average number of eggs laid daily per female from the 10th to the 13th September 1951 at an average temperature of 21°C was 12.5, from the 24th to the 30th June 1951 at an average temperature of 13°C was 5.3, whereas in the period from the 10th to the 15th October 1951 only 1.8 eggs were laid daily per female at an average temperature of 10.3°C . At temperatures between 7.5 and 8.5°C , egg laying stopped completely.

6. Parthenogenetic oviposition

T. althaeae is capable of laying eggs without having been fertilized beforehand. With respect to the number of eggs laid, no difference was found between the egg laying of unfertilized females and that of fertilized females. The only deviations were in the length of the preoviposition period which was very much shorter and, based on the average of 25 single observations, lasted only 1.3 days. It was established that from eggs laid parthenogenetically only male offspring were produced which are capable of fertilizing like any other normally produced male mites. This phenomenon is termed arrhenotoky. In this connection it would be worthwhile mentioning the investigations made by Schrader (1923) to determine the number of chromosomes of *T. urticae*. Schrader found that unfertilized eggs begin their development with 3 chromosomes. Testicles can already be recognized before the nymph stage, the spermatogonia have 3 chromosomes whereas in the ovögonia there are 6 chromosomes.

Summary

1. In most cases fertilization precedes egg laying. The position of copulation may be termed as a head-stand. The preoviposition period, between fertilization and the start of egg laying, lasted on the average 2.4 days.
2. In 97 % of all the cases observed, the eggs laid were distributed irregularly on the lower surface of the leaf, and no connection could be found between the age of the leaves and any preference shown regarding the site of egg laying.
3. The large number of eggs which on the average is 94 per female illustrates the reproduction capacity of this pest. The number of eggs laid daily is subject to considerable fluctuations which are not only caused by temperature but are also due to a periodicity within the entire phase of egg laying.
4. Parthenogenesis, which means that the development of unfertilized eggs is possible, is, however, a rare occurrence. Only males are produced from the eggs of unfertilized females. The biological purpose of this phenomenon referred to as arrhenotoky is quite clear. Any shortage of males capable of fertilizing can thus be compensated for very quickly.

The only difference between parthenogenetic egg laying and the egg laying of fertilized females was that the length of the preoviposition period was very much shorter.

D. Investigations of development and oviposition under special conditions

1. Tests on the effect of water on development and oviposition

The fact that the evaluation of the tests carried out in the outdoor laboratory was only possible when made under a provisional shelter when rain fell meant that no observations could be carried out with respect to the effect of rainfall. Therefore an attempt was made to secure conditions resembling those outdoors with natural rainfall by spraying the plants and mites with pure water. This method, however, turned out to be unsuitable because of the rapid evaporation of the water, and therefore the leaves covered by the individuals to be observed were completely immersed in water in crystallizing dishes for different periods of time.

The period of effect and the test conditions are given in the following illustrations:

a) *Influence on embryonic development*

Test commenced on August 2, 1951.

Number of eggs treated with water (laid on August 2): 48.

Period of daily effect: 4 hours (10 a. m. to 2 p. m.).

Climatic conditions during the test:

Date	Temperature in °C			Relative humidity in %	Water temperature in °C (Average of 2 measurements)
	Maximum	Mean	Minimum		
August 2	22.5	19.8	11.0	87	18.0
„ 3	26.0	19.5	16.0	80	20.8
„ 4	21.5	18.7	13.0	94	18.2
„ 5	20.0	18.0	11.5	87	18.0
„ 6	24.5	20.3	14.4	77	19.8
„ 7	22.0	18.0	14.3	77	18.2
„ 8	19.5	18.5	13.4	98	17.6
„ 9	16.5	15.0	12.0	94	15.1

Average period of embryonic development in days: 7.3 ± 0.21 .

In comparison, the period of embryonic development for untreated eggs also laid on August 2nd was found to be 7.1 ± 0.18 days representing the average of 21 single observations. By keeping the eggs of *T. althaeae* under water for 4 hours, their embryonic development was practically not delayed.

b) *Influence on post-embryonic development*

Test commenced on July 22, 1951.

Number of individuals treated with water: 25 (5 single plants each with 5 isolated larvae).

Period of daily effect: 2 hours (1 p.m. to 3 p.m.).

Climatic conditions during the test:

Date	Temperature in °C			Relative humidity in %	Water temperature in °C
	Maximum	Mean	Minimum		
July 22	24.4	17.5	8.9	74	20.3
" 23	21.0	17.5	12.6	88	19.1
" 24	16.5	14.8	11.8	91	15.0
" 25	14.5	14.0	12.5	90	14.1
" 26	17.9	14.8	8.9	92	16.2
" 27	23.1	17.0	11.5	86	19.7
" 28	25.1	19.0	12.5	74	21.0
" 29	26.0	19.1	14.0	77	21.0
" 30	27.0	21.0	16.5	81	21.5
" 31	29.7	21.0	16.2	83	21.8
August 1	28.5	22.0	15.5	90	21.5

The immersion of all development stages in water for 2 hours daily was withstood without the vital functions being affected, although the post-embryonic development of *T. althaeae* was delayed slightly. The average period of post-embryonic development of the treated individuals was 10.5 ± 0.18 days as compared with 9.6 ± 0.15 days for the untreated individuals.

c) Influence on oviposition

Test commenced on July 6, 1951.

Period of test observation: 9 days.

Number of observed females: 18.

Period of daily effect: 3 hours (11 a. m. to 2 p. m.).

Climatic conditions during the test:

Date	Temperature in °C			Relative humidity in %	Water temperature in °C	Average number of eggs laid (treated)	Average number of eggs laid (untreated)
	Maximum	Mean	Minimum				
July 6	19.6	15.0	11.0	79	17.7	3.2	3.6
" 7	24.1	18.2	11.5	77	20.5	4.4	4.2
" 8	26.0	20.5	14.3	74	21.2	5.2	5.5
" 9	21.0	16.9	13.4	88	18.8	5.6	5.3
" 10	24.7	21.2	17.3	77	20.4	5.5	6.0
" 11	27.3	21.3	13.2	90	20.8	6.8	6.5
" 12	21.5	18.4	13.3	82	19.3	4.2	4.5
" 13	21.5	16.4	10.4	80	19.4	4.4	4.2
" 14	20.7	16.2	11.4	84	18.6	3.7	4.0

The treatment of females with water did not inhibit the egg laying. The differences between the numbers of eggs laid by treated females and those laid by untreated females are within the natural range of deviation, and are so slight that hardly any use can be made of them. A point of interest is the

observation made during this test that 32 % of all the eggs were laid on the upper surfaces of the leaves which dried far more quickly following the water treatment than the lower surfaces.

2. Development and oviposition with varying supply of water to host

Three series of tests were arranged to clarify the question whether a varying supply of water to the host exercises a direct influence on the post-embryonic development and egg laying of *T. althaeae*. In selecting the test conditions it was important that the plant was offered the maximum of water on the one side and the minimum of water on the other side because only by producing extreme conditions could significant differences be expected.

a) Method

The methods adopted for this test (method of isolation etc.) are described on page 193. All 4 plants of the test series (hop shoots with roots, of the same length and the same age) were each colonized on July 1, 1951 with 5 freshly hatched larvae and 4 freshly hatched fertilized females, and the egg laying of the females and the development of the eggs was followed by daily checks.

Climatic conditions during the period of the test:

Date	Temperature in °C			Relative humidity in %
	Maximum	Mean	Minimum	
July 1	22.5	17.0	8.0	77
" 2	23.5	17.0	11.5	66
" 3	24.5	18.0	11.3	72
" 4	22.1	15.0	9.3	82
" 5	15.5	14.8	3.5	78
" 6	19.6	15.0	11.0	79
" 7	24.1	18.2	11.5	77
" 8	26.0	20.5	14.3	74
" 9	21.0	16.9	13.4	88
" 10	24.7	21.2	17.3	77
" 11	27.3	21.3	13.2	90

b) Result

The result of the investigations is given in the following table:

	1	2	3
	Hops in nutrient solution	Hops in compost soil*) — water supply (nutrient solution) adequate	Hops in sandy loam*) — water supply, minimum
Post-embryonic development in days	10.4 ± 0.15	10.3 ± 0.18	11.1 ± 0.21
Average number of eggs in 11 days	48	46	6

* diameter of pot 15 cm

With respect to the post-embryonic development and egg laying there are no significant differences between hops in nutrient solution and hops in well-watered compost soil. The poor supply of water to plants in sandy loam resulted in a slight delay of development. The influence on the egg laying of females, however, was more apparent in that 2 to 4 days after laying only 6 eggs they emigrated, or tried to emigrate, from leaves which showed chlorotic symptoms.

The difference between the behaviour of juvenile stages and that of females on the same plant may be explained by the greater need of the female for nutrition caused by the egg production and the greater demands regarding the quality of nutrition.

The result conforms with the observation made outdoors that every juvenile stage was still to be found in July on the bottom, and often strongly chlorotic leaves of the hop plants, whereas the females had emigrated to green leaves to lay their eggs (see chapter "Oviposition" on pages 205 and 206).

On applying these results to outdoor conditions the following conclusions may be drawn:

1. The test result in "sandy loam" shows that the deterioration of the nutrition conditions, such as it occurs outdoors only under extreme conditions, namely on soils with unfavourable water supply, lack of depth, combined with a high population density, can appear as a limiting factor in the change in population density of *T. althaeae*, namely by first and foremost inhibiting the laying of eggs.
2. The watering of light soils, in particular, recommended as a control measure against heavy spider mite infestation (Linke 1950, Zattler 1950) does not influence the mites directly in the sense of a control. On the contrary, the nutrition conditions for the mites themselves are improved. The effectiveness of watering which becomes evident despite what has just been said may be attributed to its plant sanitation value. The favourable state of water conditions may result in an increase in resistance caused by plant physiology. The reduction of the symptoms running parallel to this is in all probability due to the property of the plant to easily compensate for the water need increased by the sucking activities of *T. althaeae* (Günthart 1945 and Gasser 1951).

Summary

The investigations on development and egg laying under special conditions brought about the following results:

1. Short-term effect of water at summer temperatures exercised neither an inhibitive effect nor a promotive effect on the embryonic development and egg laying of *T. althaeae*; the post-embryonic development was slightly delayed.

The deduction that the gradation inhibiting influence of summer rain of slight productiveness is insignificant appears justified.

2. Poor water supply to the host has a slight delaying effect on the post-embryonic development. Under these conditions egg laying was strongly inhibited. From the results it is concluded that

1. the females of *T. althaeae* require a far higher quality of nutrition than the juvenile stages;

2. a deterioration of the nutrition conditions can appear as a limiting factor in the change in population density of *T. althaeae* by first and foremost inhibiting the laying of eggs;
3. watering recommended as a control measure particularly on light soils cannot act directly in the sense of a control.

E. Life-span and ratio between sexes

The information about the life-span of *T. althaeae* gained from outdoor observations was used to establish any relationship existing between the life-span and the environmental conditions.

The investigations on the sex ratio were carried out not only because this is of interest from a biological point of view but also because it is the prerequisite for assessing the reproduction capacity of the female.

1. Life-span of females

Under the test conditions prevailing in 1951 the average life-span of a female was 30.2 days. The maximum value was 44 days, while the minimum was registered at 23 days. Without any doubt there is a connection between temperature and life-span. Due to the large fluctuations in temperature during the observation period, it is not possible to arrive at any clear connections. If it is assumed theoretically that the total number of eggs produced per female is fixed, even though it lies within a certain amplitude of variation, and that a large number of eggs are laid daily at a persistent high temperature (see the chapter on "Number of eggs" on page 205), it can be deduced that under these conditions the life-span of the female is a short one. This train of thought is also supported by the observation that the life-span of all females calculated from the beginning of September until egg laying was well over the average, namely 38.5 days. The reason for this may be attributed to the drop in temperature from the middle of September onwards together with a decrease in the number of eggs laid daily.

The investigations show that the biological optimum (Janisch 1931), in other words the conditions of temperature and relative humidity at which the physiological death due to old age without premature mortality takes place within the shortest time and at which the greatest quantity of healthy eggs are laid, conforms with the development optimum. Those ecological conditions which permit the shortest development also enable the females to produce a maximum number of eggs.

These connections are of particular epidemiological interest. Favourable living conditions admittedly lead to a shortening of the life-span of the female but at the same time they result in an increase in the number of eggs laid per unit of time. This means that there will be a speedy increase in the population density and can thus considerably influence the progress of a gradation.

2. Life-span of the male

Methodical difficulties are encountered in attempting to make a precise assessment of the life-span of the male. In view of the much greater mobility of the male, which apart from purely morphological differences such as size may also be attributed to the greater sexual activity (search for a mate), it is difficult to keep them isolated for the required period of observations. Natural death of

males was therefore only established exactly in 13 cases. The average life-span determined from these observations was 22.3 days. The maximum was 28 days, and the minimum 17 days. It appears justified to assume that the life-span of the male is shorter than that of the female.

In consequence of this short life-span, theoretically the proportion of females to males must always be in favour of a higher female percentage. This, however, counteracts the arrhenotoky occurring in parthenogenesis (see "Ratio between sexes" on page 212). The shorter life-span of the male is of no particular significance for the course of the gradation.

3. Ratio between sexes

a) Method

The egg laying of 8 females isolated on single leaves of potted bean plants was registered and determined numerically. The numbers of eggs laid per female are given in table 11. The sex determination of the 720 registered eggs was carried out in the deutonymph stage.

b) Result

The results of the investigations to ascertain the sex ratio are compiled in the following table which expresses the sexual index calculated from the ratio of males to females.

Table 11

Females No.	Eggs laid	Males hatched	Females hatched	Sexual index
1	96	34	62	1 : 1.8
2	88	28	60	1 : 2.1
3	78	24	54	1 : 2.3
4	84	25	59	1 : 2.3
5	96	29	67	1 : 2.3
6	92	27	65	1 : 2.4
7	94	27	67	1 : 2.5
8	92	24	68	1 : 2.8
Total	720	218	502	1 : 2.3

It turned out that there were considerable fluctuations in the sex ratio. No connection was established between these fluctuations and the conditions prevailing outdoors. In all cases there was a higher percentage of females. On working out the average for all the observations the proportion of males to females was found to be 1 : 2.3 with a natural range of deviation of 1 : 1.8 to 1 : 2.8. The result more or less conforms with the observations of other authors; e.g. Gasser (1951) arrived at a sex ratio of 1 : 2, while that of Worsham (1910) was 1 : 3.

Although the percentage of males is low, it is sufficient to ensure the fertilization of all females seeing that one male is able to fertilize several females. Added to this any shortage of males can again be quickly compensated for by parthenogenetic egg laying which only produces males. Epidemiologically this higher percentage of females means that more eggs will be laid resulting in a greater reproduction capacity.

Summary

1. When considered epidemiologically, it can be concluded from the relationship between life-span and temperature arrived at in the investigations that maximum development and living conditions marked by high temperatures promote gradation in two ways: they accelerate the development and increase the number of eggs laid per unit of time by shortening the life-span of the female.
2. The life-span of the male is shorter than that of the female.
3. The ratio of males to females based on an average of 720 observations is 1:2.3. The greater number of females and the high rate of egg laying may be attributed to a high reproduction capacity.

F. Hibernation and first appearance in hop growing

Investigations in this direction were concentrated on the Hallertau population recognized by its green summer females and its orange to brick-red winter females. The reason for this was that this population represents the type occurring in the Bavarian hop growing districts, whereas the Höfchen population originates from the greenhouse and therefore did not appear suitable for studying questions connected with hibernation.

1. Observations and experiments on hibernation of the population in Hallertau

It is known from literature that *T. althaeae* hibernates as an imago (Günthart 1945, Grob 1951, Linke 1950), and that the winter females can be distinguished by their orange to brick-red colour from the green to green-brown summer females (see "Morphology" on page 188). In order to obtain some information about the factors responsible for the diapause or the appearance of winter females, particular attention was paid to the time when the winter females appeared. (The term "diapause", which generally is only used for dormant periods fixed hereditarily, does not appear applicable in this case; it would be more to the point to speak of a winter rest period brought about by external influences and which begins with the appearance of winter females.)

The observations were carried out outdoors in the hop experiment plot at the experimental farm in Höfchen. Regular leaf counts were made from August 20th onwards, and the results obtained are given in table 12.

Table 12

Date of investigation	Number of leaves examined	Number of summer females	Number of winter females	% of winter females
August 28	10	83	1	1.3
September 1	10	60	30	33
„ 15	10	34	44	56
„ 28	10	16	66	80
October 6	10	3	39	94

Fertilization of the winter females was repeatedly observed. During the first few days after emerging they did not differ in colour from the summer females, and it was not until after 3 to 8 days that they changed to their characteristic brick-red.

Even before low temperatures began to prevail their behaviour differed considerably from that of the summer females. They were more or less immobile, and their vital functions appeared to be limited to a minimum so that one can speak of a state of a cataleptic character. Egg laying by these females was not observed before the winter. In order to ascertain whether the effect of low temperatures would cause a change in this prewinter behaviour, a cold test was carried out. 3 hop leaves each colonized by 30 to 40 winter females were placed in a crystallizing dish inserted in a sheet metal trough, 24 cm in diameter and 8 cm deep. The test temperature of -15°C was obtained by a freezing mixture made up of ice and cattle salt poured into the crystallizing dish. A glass funnel placed with its outlet pointing upwards prevented any direct contact between the freezing mixture and the test material. The temperature was kept constant by renewing the freezing mixture twice during the 5 hours the test lasted. The temperature was checked by means of the thermometer inserted in the outlet of the funnel.

This test is illustrated in Fig. 5.

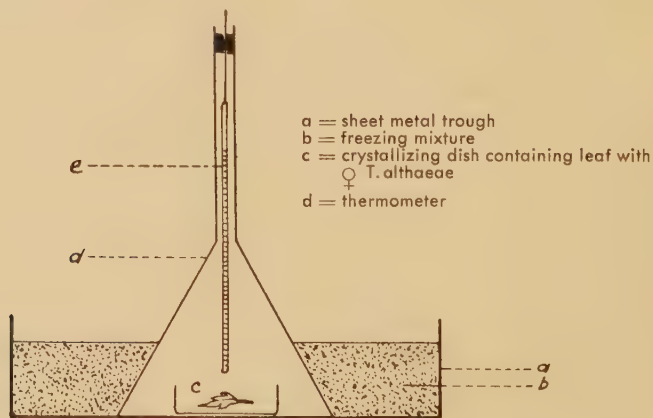


Fig. 5. Illustration of the cold test

On completion of the experiment the leaves covered with the winter females were examined under the binocular lens in the laboratory at room temperature. After 8 minutes every individual recovered from its palsy *ex frigore*.

To establish whether there would be any after-effects, 15 winter females were taken from each leaf and transferred to potted bean plants and kept under observation in the insect breeding room for a further 4 days at a temperature of 25°C . It was found that each female had recovered from the cold shock without suffering any harm. Within 36 hours the winter females formed colonies in the corners of the leaves where they remained immobile. Not a single instance of egg laying was observed.

Only suppositions can be made regarding the dependence of the development of winter types upon external factors. In view of the fact that according

to my own investigations winter females appeared before winter temperatures set in, the shortening of the period of daylight might be considered as being the factor responsible.

Bondarenko (1950) who carried out his investigations in Central Asia on *T. urticae*, arrived at similar conclusions. He found that a shortening of the daylight to 14 to 18 hours caused the appearance of winter females. By means of artificial shortening of the daylight in the greenhouse, it was possible to bring about the appearance of winter generations. Unfortunately, it is not possible to compare this result with my observations made in this direction due to the non-inclusion in the report of details regarding the test conditions, in particular the temperature.

In these experiments it was possible to confirm the finding of Bondarenko that winter females appear only when the juvenile stages of *T. althaeae* are subjected to the shortening of the period of daylight. Summer females transferred outdoors on October 2 from the insect breeding room did not change to winter females as a result of the shortened period of daylight but instead continued to lay their eggs until the zero point of development was reached.

The first winter females appeared in Höfchen on August 28. According to what has previously been said, the change must have taken place during the post-embryonic development, in other words between August 17 and 28. The average temperature during this period was 16.3°C and the period of daylight (SA to SU) lasted 14 hours. The shortening of the daylight period to 14 to 18 hours quoted by Bondarenko as being the period capable of effecting a change does not apply to Central European conditions. The question whether the shortening of the day is effective either as a result of a reduction in the quantity of light or as a result of a decrease in the amount of heat per day has not yet been answered.

To clarify the question of a possible temperature effect, 30 summer females were isolated on potted bean plants on September 15 and taken into the insect breeding room (25°C). The period of daylight was limited to 10 hours by darkening the experiment plants under a wooden frame covered with a sheet of black paper impermeable to light. The purpose of this was to determine whether winter females would be produced from the eggs laid under these dark conditions with a short period of daylight, although it should be mentioned that the prevailing temperatures were higher than outdoors. The check carried out on October 4 revealed that from all the eggs laid only summer females had been produced despite the fact that the period of daylight had been shortened considerably. It may be concluded from this that the effect caused by the shortening of the daylight period is counterbalanced by high temperatures.

Gasser (1950) arrived at different results with regard to the formation of winter types of *T. urticae*. On the basis of his investigations and with reference to the experiments carried out by Reiff (1949), he attributes the appearance of winter females to the leaf metabolism of the plant hosts. Reiff (1949) maintains that the change of colour to vermilion is due to a change in the consumption of nutrition. Under similar conditions, he carried out observations on primroses, and on counting the insects he found that the proportion of summer females to winter females on fresh green leaves was 1:1, on withering, yellowish leaves 1:2, and on partly dried leaves 1:9. Gasser (1951) reports that he can effect a change of summer females to the winter form at any time within a period of 5 to 7 days by transferring them to withering leaves. The results of the investigations carried out by Gasser and Reiff do not conform with those

obtained in my own investigations. Admittedly these investigations do confirm that the colouring of mites is dependent upon the nutrition (see chapter on "Morphology" on page 188). Summer females transferred to withering leaves in my experiments emigrated.

I was not able to effect a change of the winter type to the summer type in my experiments, which according to Gasser is a slow procedure and is not always completed. On December 3 after the first ground frosts had set in, winter females placed on green plants at room temperature were at first active but within a period of 24 hours they retired into the corners of the leaves where they formed colonies and remained immobile. Not a single case of egg laying was observed.

Despite the fact that these results are contradictory, the possibility should not be ignored that the nutrition factor, perhaps in connection with the light factor, exercises a certain influence on the appearance of winter females, especially as my own leaf counts made in autumn often showed a higher percentage of winter females on yellow leaves. It is probable that under the influence of the decreasing light intensity the quantity of chlorophyll in the leaf changed in favor of the carotene, which under certain circumstances would explain the change in colour.

The difficulty in solving questions concerning hibernation is due to the constantly varying conditions outdoors which only enable with difficulty an elimination of the light, temperature and nutrition factors whereas the results obtained from the laboratory and thermostat experiments under set conditions can only be applied outdoors with limitations.

2. Location of hibernation

According to my own observations the majority of winter females hibernated in the soil. More than 300 females were counted per hop plant; they had formed together in colonies as far down as 10 cm below the earth surface. Males and juvenile stages were not found.

The emigration of the females from the plants began in Höfchen on September 28 and ended on November 1. From papers written by other authors it is evident that the soil is not the only winter quarter for *T. althaeae*. Jary (1935) reports that a large number of winter females can overwinter in the cracks of the hop stems, and he goes on to say that these insects prefer to take shelter within the vicinity of the soil anywhere up to a height of 4 feet; in some cases as many as 500 mites were counted per stem. My own observations in the Hallertau showed that in young hop plantations where spruce branches were used as provisional supports, the winter females had taken up their winter quarters in large numbers under the bark of these spruce branches. Linke (1950) mentions that in earlier times the coconut strands used to tie the hop plants were often selected by *T. althaeae* for their winter quarters.

Seiffert (1951) reports on investigations he carried out in this connection on red clover showing that the majority of the overwintering mites had taken shelter under wilting leaves on the ground, whereas 5 % remained on green leaves.

In contrast to this, Janson (1920) and Zacher (1920) speak of adult females being found on green plant parts even during severe periods of frost. Hanstein (1901) also mentions that there is hardly any interruption in the nutrition consumption of *T. althaeae* during mild winter weather.

Such observations were made neither in Höfchen nor in Hallertau. My own investigations showed the soil to be the only winter quarter preferred by *T. althaeae*.

The losses of overwintering stages can assume considerable proportions as shown by the following observations. Clods of earth taken from outdoors and colonized with winter females were examined under the binocular lens in the laboratory on December 29, 1951 at a temperature of 25° C. The percentage of dead females varied between 15 and 45 %. It is highly probable that this percentage increases as the winter goes on, because the winter types, more than any others, are subjected to unfavourable meteorological conditions. Considering the large numbers of females overwintering per plant and the large numbers of eggs laid by *T. althaeae*, these losses are of no great significance from an epidemiological point of view.

3. Observations on autumn behaviour of the population in Höfchen

Seeing that all investigations carried out in connection with hibernation were concentrated on the Hallertau population, similar observations made with the Höfchen population were only of an informative character and will therefore only be described in summary form.

a) In contrast to the Hallertau population whose brick-red winter females can be clearly distinguished from the green summer females, no externally recognizable winter females appeared in the Höfchen population even in late autumn (last observation on November 2). At this time all the females of the population still had the same carmine-red colour which they had throughout the summer (see "Morphology" on page 188).

b) Despite a shortening of the period of daylight and drops in temperature from the middle of September onwards, the females displayed no change in their biological behaviour, and continued laying eggs until they reached the zero point of development (see chapter on "Oviposition" on pages 205 and 206). Reference will be made to the epidemiological conclusions resulting from the above in the discussion on the change in population density of *T. althaeae*.

c) All stages of *T. althaeae* were still to be found on the leaves on November 2, at a time when the greater part of the hop foliage had already died off. All individuals were in a state of rigidity due to cold from which they immediately recovered on being moved to the laboratory at 20° C. Within 3 hours the hatching of many teliochrysalis stages was observed. The females, which were immediately fertilized, died within 1 to 2 days after being isolated on bean plants and laying an average of 5 eggs.

The question whether and in what stage the Höfchen population originating from the greenhouse is capable of overwintering outdoors has still to be clarified.

4. First appearance

The date of the first appearance of *T. althaeae* in spring depends upon the ecological conditions. It is to be assumed that the atmospheric and soil temperatures — conforming to the various overwintering possibilities of *T. althaeae* — are decisive for the date when the winter females awake from their dormant state and recommence their normal activities.

Many years of observations in the Hallertau have shown that on the average the appearance of winter females on young hop plants may be expected towards

the end of April to the middle of May. A guide to the temperature conditions required for this appearance is given in the monthly average values worked out by the meteorological station at Hüll for 1926 to 1950. According to these figures the atmospheric temperature in April was 7.4° C (average maximum 13.5° C); in May 11.9° C (average maximum 18° C), whereas the soil temperatures for the same months at a depth of 20 cm were 9° C and 14.1° C respectively.

Exact observations were made to establish the date when the winter females first appeared on hops in the Hallertau in 1951. The first active winter female was seen on April 23. At this time the young hop shoots were about 5 cm long. The females did not begin to lay their eggs until after the leaves had started to develop so that it appears justified to assume that a prerequisite for this is the resumption of the sucking activities. The emigration of the winter females to the leaves was not sudden but took place progressively and, under the conditions prevailing in 1951, lasted from 6 to 12 days. The daily average temperatures of the decade preceding April 23 fluctuated between 7.5 and 14° C.

Even though no general valid conclusions can be drawn from these observations with respect to the temperature conditions necessary for the first appearance of winter females because not only the average values but also the maximum are of significance for the resumption of the insects's activities, they do permit the questionable temperature range to be narrowed down and the effective temperature range to be approached. Apart from the temperature, it would appear that other factors, above all the period of daylight, exercise an influence on the appearance of winter females in spring. This is indicated by the experiments carried out during the course of the winter in which egg laying by winter females in the laboratory at temperatures around 20° C was not observed either after cold shock (see chapter on "Hibernation" on pages 213 and 214) or after the setting in of ground frosts. An explanation for this would be, apart from the shortened period of daylight under these conditions, the sudden difference in temperature to which the winter females were subjected in these tests and to which the natural conditions, under which a gradual increase in temperature sets in in spring, do not comply. In all probability the temporal effect of low winter temperatures, which are difficult to reproduce in laboratory experiments, also plays a certain role.

A previous colonization of intermediate hosts such as was observed by Chapman and Lienk (1950) for *T. bimaculatus* Harvey in fruit growing and by Wilhelm (1951) for *T. althaeae* v. Hanstein in viticulture, is only a seldom occurrence with *T. althaeae* in hop growing due to the soil preparation carried out in spring and the resultant weed destruction, and further because of the early growth of the hop plants, even though winter females as well as eggs laid by these were found on typical hop weeds in several hop plantations in the Hallertau in the spring of 1951.

Summary

The observations and tests regarding hibernation and the first appearance of *T. althaeae* were carried out chiefly on the Hallertau population with the following results:

1. The dormant period of *T. althaeae* begins with the appearance of winter females which are distinguished from the green coloured summer females by their orange to brick-red colour and also by the cessation of egg laying.

The chief cause for the appearance of winter females already observed before winter temperatures had set in appeared to be a shortening of the period of daylight which was only effective when the juvenile stages were subjected to it.

High temperature, under set conditions, can counterbalance the effect produced when the period of daylight is shortened.

The egg laying of winter females could not be caused artificially by cold shock.

2. According to my own observations, *T. althaeae* showed a preference for the ground as its winter quarters. Emigration from the plant hosts began on September 28.
3. Observations carried out on the autumn behaviour of the Höfchen population were merely of an informative character. In contrast to the Hallertau population, no winter females of the Höfchen population were recognized by a change in colour.
4. The soil and atmospheric temperatures are of significance for the date when the winter females first appear in spring. It appears possible that the period of daylight also exercises an influence.

VII. Investigations into the epidemiology of *Tetranychus althaeae*

The purpose of these investigations was to gain an insight into the complex of questions raised by the epidemiological behaviour of *T. althaeae*, and also to contribute to the assessment of the population-dynamic factors.

1. Number of generations

The number of generations developing within the unit of time is of decisive significance for the epidemiological behaviour of *T. althaeae*. In this connection *T. althaeae* may be termed as being polyvoltine which means that the number of generations occurring within a certain period of time is not determined genetically but depends upon the environmental conditions. In view of this it is quite understandable that the data given by various authors regarding the number of generations occurring in a year deviate considerably. Garlick (1929) reports that under the conditions prevailing in Canada there are more than 6 generations per year, Bondarenko (1950) observed under Central Asiatic conditions the appearance of 12 to 17 generations in a year; Chapman and Lienk (1950) ascertained in observations carried out in Western New York that there are 8 generations in a year, whereas according to Linke (1950) there are 5 to 9 generations per year in Bavaria.

In the next part of this chapter a survey will be given of the temporal sequence of generations appearing under the meteorological conditions prevailing at the place where the experiment was carried out, whereby it should be mentioned that the figures given are the maximum numbers of generations without taking overlapping into consideration even though this occurs regularly. The reason for this overlapping is due to the fact that from the first eggs laid by a female puberal females of the second generation have already developed while females of the first generation are still continuing to lay eggs. This process is repeated in every generation and provides an explanation for a population of *T. althaeae* being composed of several generations occurring together.

The time from one egg laying to the next was assumed as the generation period. The investigations described here were carried out on the Höfchen population.

The methods adopted for isolating the females and the larvae and recording the temperatures were the same as those described in the chapters on "Post-embryonic development" and "Embryonic development" (pages 193 and 201—202).

Seeing that the first appearance of *T. althaeae* is to be expected at the end of April to the middle of May, the time selected to start the observations and the experiments (May 21) was rather late because it does not fully conform with natural conditions. Technical difficulties, however, did not permit the observations outdoors to be started any earlier.

	First egg laying		First hatching of larvae		First imago
First generation	May 21		June 2		June 14
		12 days 13.8° C		12 days 15.9° C	
Second generation	June 16		June 25		July 8
		10 days 16° C		13 days 15° C	
Third generation	July 10		July 18		July 29
		9 days 17° C		11 days 16.5° C	
Fourth generation	August 1		August 7		August 19
		7 days 19.4° C		12 days 15.8° C	
Fifth generation	August 21		August 29		September 8
		9 days 16.4° C		10 days 16.8° C	
Sixth generation	September 10		September 17		October 7
		8 days 18° C		20 days 12° C	

The 7th generation, eggs of which were laid on October 11, was not able to develop fully and remained in the egg stage. The table shows that under the conditions prevailing in 1951 six generations of *T. althaeae* were able to develop at the place of observations between May 21 and October 7.

It is highly probable for 7 to 9 generations to occur in one year when the first appearance of the mites takes place early in the year and the weather conditions are favourable, such as prevail in "mite years".

2. Change in population density

As soon as pathogenic organisms occur in relatively large numbers in a culture, they develop into a biological and an economic problem. The absolute number of individuals per unit of area, which justifies using the term "population density", fluctuates according to the type and size of the pest.

The question regarding insect infestations and their causes is just as important as the question regarding change in population density. By this one understands the total of appearances beginning with an increase in the population up to the climax of the population density until it begins to decrease.

The purpose of the phenomenological-statistical investigations described in the following was to determine the cause of the change in population density of *T. althaeae* under the special conditions prevailing in Bergische Land and the Hallertau in 1951. Even though this method, intended to provide a picture of the numerical evolution of a complete population by carrying out regular leaf counts (colonization analysis), is not sufficient in itself to eliminate the individual significance of each of the many population-dynamic factors, its results, by supplementing the individual observations on isolated mites, do contribute to an understanding of the epidemiological behaviour of *T. althaeae*.

a) *Observations on change in the population density in Höfchen*

aa) Method

On May 20 six hop plants from the hop experiment plot were each infected with 30 females of the Höfchen population. From each of these plants 6 leaves were taken and counted at temporal intervals as indicated in Graph 3. Only females were counted because in this way the figures obtained suffice to illustrate the fluctuations of the numerical evolution of the population. Therefore the infestation figures on which the graph has been based are only of relative significance and do not give any information as to the absolute density of the infestation. It is equally clear that the graph for the change in population density illustrated below only gives the seasonal change in population density for the special conditions prevailing in 1951 and is not valid generally.

bb) Result

The result of the counts is given in Graph 3 which also shows the meteorological conditions during the period when the observations were carried out.

The following can be deduced from the phenomenological-statistical observations made in Hallertau in 1951.

1. The infection on May 20 1951 was successful; the reproduction and propagation of *T. althaeae* occurred in the manner described despite relatively unfavourable meteorological conditions.

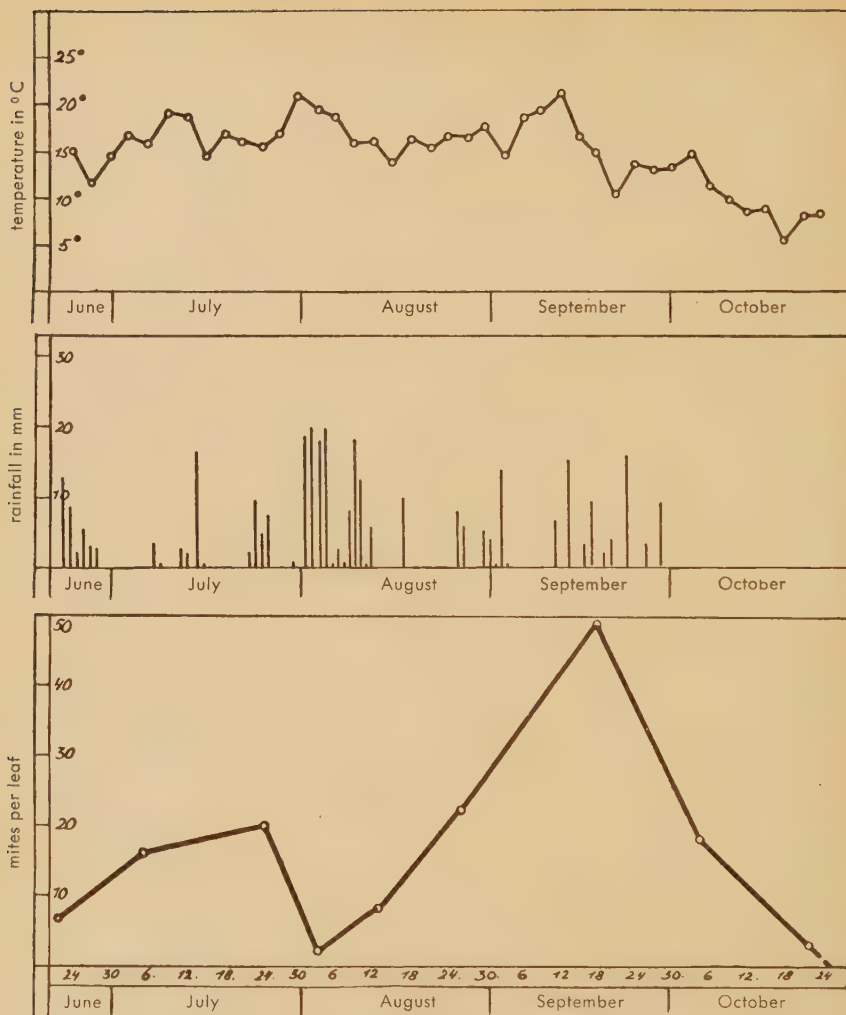
2. The observations confirm experience gained in the field to the effect that the infestation starts at the bottom of the plants and works its way upwards. It was decided not to express numerically the progress of infestation for each individual plant because the speed of migration and propagation upwards depends upon the change in population density from year to year, and is therefore subject to large fluctuations.

3. Although the test plot was left completely untreated, natural enemies did not occur to any extent worth mentioning.

4. Any external injury to the growth of the test plants as compared with the non-infected plants was not observed. The observed population evolution cannot therefore be termed as mass reproduction in the strict sense of the word.

5. The general trend of the curve illustrates the constant increase in the infestation density until July 25, 1951. The rapid drop on August 3 may be attributed to the effect of a thunderstorm on July 31 and August 1 which produced a rainfall of 18.7 mm within 1½ hours at a wind velocity of 40 km per hour.

Graph 3

Progress of the change in population density of *T. althaeae* in Höfchen in 1951

The total rainfall on both days amounted to 38.7 mm. Seeing that no dead females were found on the leaves, while dormant stages and eggs were present in large numbers, it is to be assumed that the heavy and sudden decrease of the infestation density is due to the females being washed off the plants. This may be explained by the fact that because of their size and weaker powers of mobility the females are more exposed to the influence of rain water than the eggs and dormant stages which seek protection under the leaf ribs and under the web, added to which they adhere to the lower surfaces of the leaves. The fact that the dormant stages and the eggs survived the downpours of rain without being

injured is the reason why the infestation increased again to 22 females per leaf by August 26. The climax of the infestation, as a result of the rise in temperature and only short periods of rainfall (at the beginning of September), was reached on September 18, in other words at a time when normally the vegetation of the hop has already been concluded or the hop has reached its physiological maturity. This increase in infestation confirms the result of the isolations outdoors which during the same period and at the highest average temperature of the whole period of observation exhibited the shortest period of development with maximum egg laying. From the end of September onwards the infestation began to drop heavily due to the low temperatures. It reached its lowest point on October 22 following continued emigration of the females.

An amazing similarity to the investigations described in this paper is revealed in investigations carried out by Chapman and Lienk (1950) particularly with respect to the culmination point and the decrease in infestation. In their investigations which they carried out in Western New York on fruit bushes with *T. bimaculatus* (= *T. althaeae*), the highest infestation figure was recorded on September 10 with 110 mites per leaf. During the following period the population was reduced to 2 mites per leaf by October 30.

b) Observations on change in the population density in the Hallertau

As the investigations on the change in population density in Höfchen were carried out with the Höfchen population, distinguished by red pigment, it appeared expedient in order to complete the picture also to register in a similar manner the numerical evolution of the Hallertau population under the ecological conditions of the Hallertau. The method adopted was the same as that described in the previous chapter. It is worth mentioning that not only the females but also all the other active and dormant stages were included in the leaf counts made in the Hallertau.

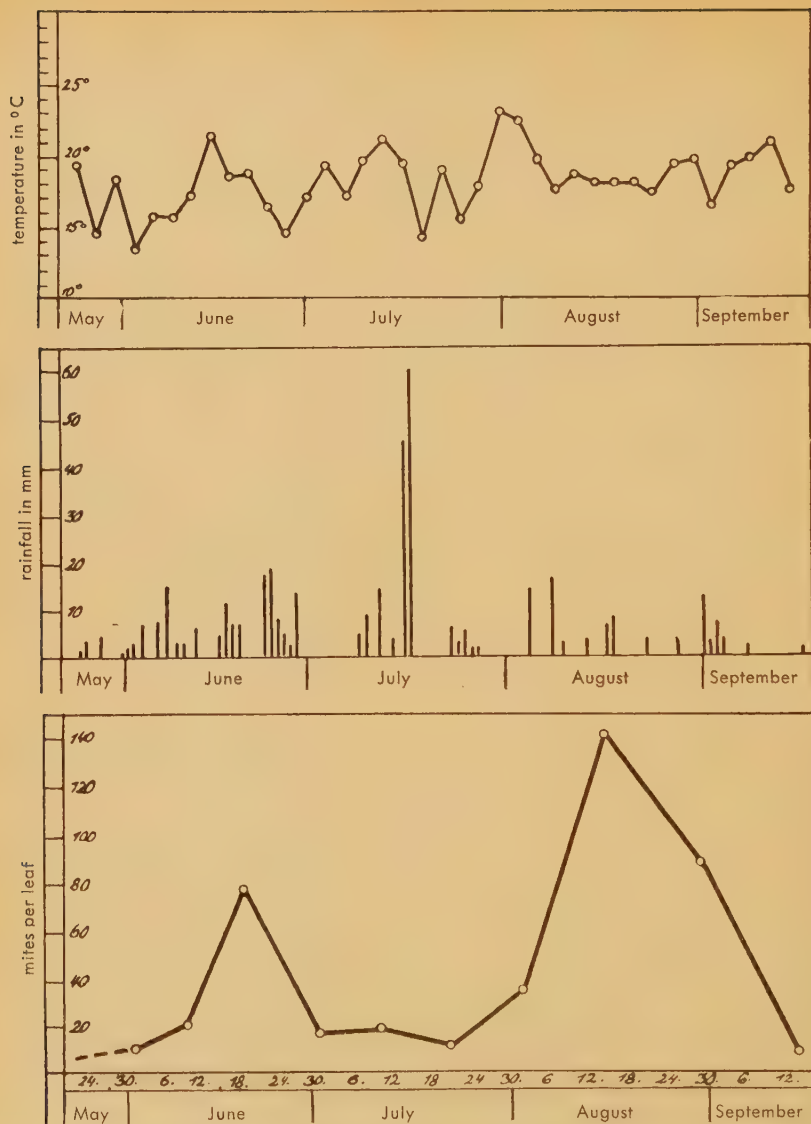
The observations were carried out on 10 untreated plants growing in a hop garden near Wolnzach (Upper Bavaria). The progress of the population evolution is shown in Graph 4 which also depicts the meteorological conditions prevailing during the period of observation.

The graph shows that there was a heavy reduction in infestation from 76 mites per leaf on June 20 to 16 mites per leaf on July 1, this being attributed to the heavy rainfall between June 20 and June 30 and the considerable drop in temperature. The heavy rainfall in the following period prevented a rapid increase in infestation. The fact that the heavy rainfalls on July 15 and 16 which together produced 110 mm did not lead to a heavier decimation is due to the method adopted for the leaf counts which were far less affected by rain washing off the mites because in these counts not only females but also all the dormant stages were included. The climax of the infestation was reached on August 15 with 140 mites per leaf. This increase may be attributed to the high temperatures prevailing between the end of July and the beginning of August and the favourable effects of the slight rainfall during this period.

On comparing the two curves for change in population density obtained under different ecological conditions and for different varieties it is seen that there is:

1. conformity in the gradation promoting effect of the temperature and
2. conformity in the development and gradation inhibitive effect of the rain.

Graph 4

Progress of the change in population density of *T. althaeae* in the Hallertau in 1951

There is, however, an obvious difference on comparing the temporal drop of both curves. Whereas in the case of the Höfchen population this did not begin until the end of September (see curve for change in population density for Höfchen), the infestation in the Hallertau already began to drop at the end of August reaching its lowest point for the period of observation at 9 mites per leaf. The

reason for this is not due, as might be presumed, to a gradual deterioration in the nutrition conditions but to the different behaviour of both varieties described in the chapter on "Hibernation" (page 217). The appearance of winter females in the Hallertau population from the end of August onwards is connected with the cessation of egg laying and reproduction.

c) Active and passive propagation

The active and passive propagation is closely related with the problem of the change in population density of *T. althaeae* in which a part is played by the population evolutions not only according to time but also according to sites.

Seiffert (1951) comments on American papers dealing with this problem and in which considerable significance is attached to passive propagation by the wind. Andersen (1948) also examined with *P. pilosus* the transfer of mites as caused by the wind, and found that the number of mites dispersed in this manner which he caught on glass plates coated with vaseline was quite considerable. At a wind velocity of 4 metres/sec. converted to hours and square metres, he observed the dispersal by the wind of 400 mites.

Apart from this passive propagation, it was also found on several occasions that the active propagation of *T. althaeae* is enhanced by migration on the ground. The examinations carried out by Seiffert (1951) show that although the mites are extremely small they are capable of covering considerable distances. In the laboratory he established speeds of 4.5 to 8.5 cms. per min., and outdoors he observed cases where *T. althaeae* emigrated from clover fields to neighbouring potato fields when changing its host.

On applying these results to *T. althaeae* in hop growing, it can be concluded beyond all doubt that dispersal by the wind can play a part in widening the area of infestation both from garden to garden as well as within the same hop field. The active propagation of the mites resulting mainly from a lack of nutrition is only of minor importance in hop growing.

d) Experiment to assess the factors producing changes in population

There is no unanimity in literature regarding the assessment of the so-called population-dynamic factors exercising an influence on the change in the population density of insects. The difficulties arising in this connection which are due to the complex nature of the problem as a whole also apply to the change in the population density of *T. althaeae*.

According to Zwölfer (1930), the fluctuations in the population density of a species are mainly determined by the relationship between procreative power and environmental resistance. Whereas the biological and epidemiological investigations clearly illustrate the connection between the procreative power, resulting from the percentage of females and the average number of eggs laid, and the temperature, as well as the gradation-promoting influence of high temperatures (see chapters on "Post-embryonic development", "Embryonic development", and "Oviposition"), it is practically impossible to clearly assess the factors responsible for environmental resistance. The natural enemies are the most important among the mortality factors of a biotic nature dependent upon density. Opinions differ considerably concerning the importance of these natural enemies as a limiting factor in the change in the population density of *T. althaeae*. Vitzthum (1943) and Geijskes (1938) emphasize that the activity of natural enemies would not be sufficient to hold up a mass reproduction of Tetranychidae. They do point out, however, that the useful insects should be protected wherever possible. Huffacker and Spitzer (1950) reported that

a mass appearance of *Chrysopa californica* resulted in the mites being considerably decimated although damages felt economically could not be prevented. Russian authors, on the other hand, attach great importance to the predators of *T. urticae*; they established that *Scymnus punctillum* decimated spider mites occurring on cotton plants to such a considerable extent that it was not necessary to carry out a chemical control. M o r s t a t t (1923) contends that success in the control of biological pests can only be expected where insects are carried to new areas without being accompanied by their natural enemies. In hop growing itself no case is known where the occurrence of useful insects has prevented a mass reproduction of *T. althaeae*.

These differences of opinions demonstrate the difficulty experienced in obtaining a clear assessment of the whole problem which after all is due to the fact that it is impossible to assess quantitatively the factors with which we are acquainted by means of experiments. Even if this were possible in individual cases, results obtained from such experiments and observations could not be applied in general to field work. It should not be forgotten that the useful insects are just as sensitive to ecological factors as the pests and that their influence differs from year to year.

Apart from this, and while on the topic of the effectiveness of useful insects, several other points might also be mentioned. There is hardly a single specialist among the known predators of *T. althaeae*, i. e. a predator which specialises on one particular species of pests. In view of this, although nourishment is always to be found, the effect on the individual pest species cannot be as great as would be the case if a predator were to specialise, unless there were only one species of pest present. This, however, is seldom the case in hop growing with its relatively wide range of pest fauna. In this connection it is pointed out that the two enemies most frequently mentioned in literature, *Scymnus punctillum* and predatory bugs, do not occur in large numbers until about the middle of July (A n d e r s e n 1948) which means that their influence is first felt during the third spider mite generation. At this time, however, the pest has normally entered into the stage of mass reproduction.

Regarding the assessment and significance of the food factor, the conditions are similar. Considering the rate of growth and the large vegetative apparatus of the hop plant, its restricting influence can only be rendered effective in years with an extremely high population density; it should however be taken into account that even in this case *T. althaeae*, in view of its wide range of host plants, always has the possibility of emigrating to hop weeds which make suitable hosts (see chapters on "Host plants" and "Influence of a varying supply of water to host" on pages 189 and 209).

The abiotic factors of the environmental resistance, which are not dependent upon density, are far more significant for the progress of the population evolution of *T. althaeae*. The chief factor is the climatic influence.

Low temperatures act upon *T. althaeae* by delaying development and reducing the egg production, although they can hardly be considered as absolute mortality factors.

The significance of rain as a factor inhibiting the gradation and governing the mortality of *T. althaeae* is to a large extent dependent upon the other conditions.

Apart from the fact that in most cases rainfall brings a drop in temperature with it, wetting of the lower surfaces of the leaves for the time it is effective puts a stop to all vital activities of *T. althaeae*. Even though the experiments

show that all stages of *T. althaeae* are able to withstand immersions under water for a number of hours, they are just the same inhibited in their ability to move about and to consume food during this period. The delay in development caused by this depends upon how long the effect lasts. Accordingly, short periods of rain exercise no noteworthy influence (see graph depicting increase in the change in population density for Höfchen in September, and increase in infestation for the Hallertau at the beginning of August).

On the other hand long periods of rain may decimate the infestation to a considerable extent (see decrease in infestation for Hallertau at the end of June, and for Höfchen at the beginning of August). This rainfall is all the more effective as a mortality factor when the temperatures prevailing at the time are correspondingly low (see laboratory investigations on the "Influence of extremely high relative humidity" on page 198).

For this reason the rainfall in May, in conjunction with the temperatures prevailing at that time, plays a decisive role in the assessment of the expected population progress of *T. althaeae*, as already established by Zattler (1936). Added to this is the fact that a decimation of the first generation curtails the potential development of *T. althaeae* much more effectively than would be the case in a later generation.

Zattler points out that in years when the average daily temperature in May is 13° C and over, and when the amount of rainfall in the same month does not exceed 50 to 70 mm, the conditions favour a heavy and dangerous occurrence of copper stain, whereby the numbers of overwintering individuals do not exercise any great influence.

In assessing the rain as a mortality factor, it should be mentioned that the active stages only differ gradually in their reaction to moisture, which means that in this connection one cannot speak of a "critical point" in the development of *T. althaeae*, while the egg and the chrysalis are the stages most insensitive to rain. In view of these differences and the comprehensible fact derived from the study of the biology of *T. althaeae* that all stages always occur together, it is seen that the mortality producing effect of rainfall is also subject to natural limits. This contention is supported by the course of the change in population density graphs (Höfchen, Hallertau) which showed that rainfall may have a considerable influence on the population evolution but that it never leads to a complete extermination, or if so only under the most extreme conditions.

In summarising it may be established with respect to the gradation inhibiting effect of the rain that this is dependent upon the time it lasts, its intensity, and the temperatures prevailing at the time.

It is seen from what has been said above that among the population-dynamic factors the weather with its components temperature, relative humidity and rainfall exercises the greatest influence on the population evolution of *T. althaeae*, particularly as it is not only able to promote gradation but also to act inhibitably.

This is confirmed by statistical records which clearly show that the mass reproduction of this pest spread itself over wide areas in the so-called mite years (1934, 1950) which were marked by hot and dry weather.

The only possible cause for this phenomenon comprises the effects of uniform, one-sided climatic conditions prevailing over a large area, i. e. the reduction of the abiotic environmental resistance.

Summary

The investigations on the epidemiology of *T. althaeae* produced the following results:

1. *T. althaeae* is polyvoltine. The number of generations occurring in the unit of time depends upon the ecological conditions. In 1951 six generations developed in the period from May 21 to October 7. A demarcation between the individual generations is only possible in theory.
2. The observations on the change in the population density of *T. althaeae* were carried out on two populations and at two different places. Both gradation graphs obtained as a result of regular colonization analyses made in the hop fields of the Hallertau and at the experiment farm at Höfchen show without any shadow of doubt that a change in population density is decisively influenced by abiotic factors. While first and foremost high temperatures must be held responsible for the increase in infestation density, productive and persistent rainfall is the most important gradation inhibiting factor and its effectiveness is all the greater when the prevailing temperatures at the time of the rainfall are correspondingly low.

VIII. Summary of the principal results

The investigations carried out on *Tetranychus althaeae* v. Hanst. in 1951 produced the following principal results:

1. There is no fundamental difference between the epimorphosis of the male and that of the female of *T. althaeae*. The shorter development period of the male is due chiefly to a shortening of the deutonymph stage.
2. All the vital functions of *T. althaeae* are first and foremost dependent upon the temperature. This applies in particular to the rate of the embryonic and post-embryonic development.
3. The values for the rate of development of *T. althaeae* obtained at constant temperatures do not coincide with the results obtained at corresponding average temperatures outdoors. An acceleration of development was observed regularly under the changing conditions outdoors. The causes of this can only be assumed, but are not definite.
4. The period of post-embryonic development was influenced by varying relative humidity. Optimal conditions prevail when the relative humidity is below 70 %.

100 % relative humidity persisting over a long period together with liquid water on the lower leaf surfaces of the test plants acted strongly inhibitive on the post-embryonic development of *T. althaeae*. The death of this pest occurred all the more earlier as the prevailing temperatures dropped.

The influence of varying relative humidity on the period of embryonic development is so minute that practically no use can be made of it.

5. Short-term action of water at summer temperatures does not exercise an inhibitive influence on the embryonic development and oviposition of *T. althaeae*. The post-embryonic development was delayed to a slight extent.
6. A lack of water supply to the plant host resulted in a slight delay of the post-embryonic development. The oviposition of females was strongly inhibited.

7. Under outdoor conditions the average number of eggs laid by a female of *T. althaeae* was 94 (maximum 128, minimum 73).

On the average the preovipositional period lasted 2.4 days. The number of eggs laid daily fluctuated considerably.

8. Parthenogenesis is possible. Only males were hatched from the eggs of unfertilized females. The preovipositional period was shortened when the eggs were laid parthenogenetically.
9. The ratio of males to females hatched out of fertilized eggs was 1 : 2.3.
10. On the average a female lived 30.2 days outdoors (maximum 44 days, minimum 23 days). The life-cycle of the male is shorter, lasting on the average 22.3 days (maximum 28 days, minimum 17 days). High temperatures shorten the life-cycle of the female thus increasing the number of eggs laid per unit of time.
11. The winter rest period of *T. althaeae* starts with the appearance of winter females characterized by their brick-red colour and cessation of egg laying. It is presumed that the winter type is dependent upon photoperiodism. An influence on food is not excluded. The soil is preferred by *T. althaeae* as its winter quarters.

The soil and atmospheric temperatures are of significance for the time when the pest makes its first appearance in spring. It appears possible that the period of daylight also exercises a certain influence.

12. *T. althaeae* is polyvoltine. The number of generations developing within the unit of time depends upon the ecological conditions. Under the conditions prevailing at the place where the experiments were carried out, *T. althaeae* occurred in six generations in 1951.

The epidemiological behaviour is marked by the reproduction potential ensuing out of the higher percentage of females and the large number of eggs laid, with the result that when the living conditions are favourable *T. althaeae* is able to pass very quickly into the mass reproduction stage. The progress of the change in population density is decisively influenced by abiotic factors.

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